La zone hyporhéique favorise la résilience des communautés d'invertébrés dans les rivières alluviales intermittentes : expériences de terrain et mésocosmes en laboratoire

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THE HYPORHEIC ZONE AS A PRIMARY SOURCE OF INVERTEBRATE COMMUNITY RESILIENCE IN INTERMITTENT ALLUVIAL RIVERS: EVIDENCE FROM FIELD AND MESOCOSM EXPERIMENTS

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Abstract

Understanding how communities respond to disturbance is essential to identifying processes that determine their assembly and to predicting the future effects of climate change on biodiversity and ecosystem functions. Drying (*i.e.* complete loss of surface water) is a natural disturbance affecting 50% of rivers worldwide and is increasingly occurring in perennial rivers due to climate change. Drying also represents a major challenge for aquatic communities in most river systems. However, its effects on communities and the underlying processes contributing to their resilience (*i.e.* return to pre-drying levels) have not been well quantified in environmentally harsh ecosystems, such as alluvial rivers. In these systems, communities could be less affected by drying because they are composed of resistant and resilient species filtered from the regional species pool. In this thesis, I addressed the resilience of aquatic invertebrates–a ubiquitous group involved in key ecosystem functions–to drying in alluvial rivers. I used 4 congruous field and mesocosm experiments to quantify resilience and identify its primary sources. First, I found no differences in taxonomic richness, abundance, composition and functional diversity between drying reaches and those in perennially flowing reaches across 8 alluvial rivers, even after as few as 19 d post-flow resumption. This suggests that in alluvial rivers (i) harsh environmental conditions filter all but resistant and resilient species from local communities and (ii) the mosaic of perennial habitats, including the underlying hyporheic zone, promotes resilience by providing proximate sources of colonists. Second, I identified the primary source of colonists in an alluvial river by drying reaches and manipulating/quantifying colonization processes (*e.g.* drift). Blocking drift did not affect the resilience of communities, which all recovered within 1–2 wk, and evidence suggested their resilience was driven by colonization from hyporheic zone. Third, I tested how harsh environmental conditions preceding drying cause invertebrates to migrate into the hyporheic zone using laboratory mesocosms. High water temperature and intraspecific competition caused *Gammarus pulex*, a common benthic detritivore, to migrate. However, reductions in their survival, feeding rate and energy stores indicated tradeoffs between tolerating harsh surface conditions and limited resources (*e.g.* food) in the hyporheic zone. Fourth, I assessed how depth of the water table (below the surface) during drying, a factor sensitive to future exacerbation of drying by climate change and water abstraction, affected 2 populations of *G. pulex*, originating from intermittent and perennial rivers, in mesocosms. Increasing water table depth diminished the hyporheic zone's role as a source of colonists by reducing survival of both populations and altered ecosystem function by decreasing in leaf litter decomposition by *G. pulex* up to 46%. Overall, my results support an emerging concept that harsh ecosystems are highly resilient and indicate that the effects of drying on biodiversity and ecosystem functions could vary across river systems. In alluvial rivers, the hyporheic zone can contribute strongly to community resilience and management should focus on protecting and restoring vertical connectivity to maximize resilience to climate change. Future studies may aim to examine how migration into the hyporheic zone during drying influences other important community processes, such as interspecific competition.

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Résumé Etendu

Un des objectifs majeurs de l'écologie des communautés est d'identifier les processus qui déterminent leur organisation, quelle que soit l'échelle spatiale ou temporelle considérée. Ces processus peuvent être déterministes, en impliquant un filtrage prévisible par des facteurs environnementaux abiotiques et biotiques des espèces du pool régional pour composer une communauté locale. Au contraire, ils peuvent être stochastiques, c'est-à-dire liés à des variations aléatoires des taux de colonisation, natalité, de mortalité et des abondances relatives des espèces.

Un paradigme émergent prédit que les perturbations influencent l'importance respective de ces processus, avec notamment une importance accrue des processus déterministes. Une sélection des espèces du pool régional devrait en retour donner lieu à des communautés très résilientes au régime de perturbation concerné. En retour, décrire et comprendre la résilience des communautés aux perturbations est un élément essentiel à la gestion et conservation de la biodiversité des écosystèmes.

L'assèchement (disparition complète d'eau en surface pour une durée donnée) est une perturbation naturelle affectant les cours d'eau dans de nombreuses régions du monde. De plus en plus de cours d'eau pérenne s'assèchent en réponse au changement global et des besoins croissants en eau. L'assèchement agit comme un filtre environnemental fort qui diminue la richesse taxonomique et modifie l'abondance et la composition des communautés aquatiques. La persistance des communautés est en grande partie expliquée par leur résilience. Toutefois, cela peut ne pas être généralisable à tous les hydro-systèmes car les communautés peuvent être plus ou moins sensibles à l'asséchement en fonction du régime de perturbations rencontré. Il s'agit du principe de co-tolérance : les communautés des cours d'eau naturellement très perturbés (*i.e.* crues, remobilisations du substrat) devraient être dominées par des taxons possédant des traits biologiques leurs conférant une résilience ou résistance élevée à d'autres perturbations tels que les assèchements. De plus, les processus sous-jacents à cette forte résilience (*i.e.* la dérive, l'oviposition, la migration verticale dans la zone hyporhéique) et leur importance respective sont encore peu étudiés, notamment à des échelles spatiales pertinentes avec celles auxquelles agissent les perturbations. Si la compréhension des processus qui favorisent la résilience des communautés est actuellement un axe majeur de recherche en écologie des communautés, elle permet aussi en d'améliorer la gestion et la restauration des cours d'eau face aux changements environnementaux futurs.

Dans cette thèse, mon objectif était d'étudier et de comprendre la résilience des communautés dans un écosystème largement répandu et naturellement très perturbé, à savoir les rivières alluviales intermittentes. Utilisant les invertébrés aquatiques comme modèle biologique, j'ai couplé différentes approches méthodologiques, allant des suivis de terrain, des expérimentations *in-situ* et des mésocosmes en laboratoire. Les résultats de ces expériences sont présentés dans les 4 chapitres suivants (chapitres 3-6):

Chapitre 3: Les communautés d'invertébrés des rivières alluviales sont très résilientes à l'assèchement. Dans cette étude, j'ai décrit la résilience des communautés dans 8 rivières alluviales du sud-est de la France. Pour cela, j'ai comparé les communautés d'invertébrés aquatiques avant et après des assèchements modérés (2-3 semaines) et sévères (1-3 mois) dans des tronçons pérennes. Je n'ai trouvé aucune différence de richesse taxonomique, composition ou diversité fonctionnelle des communautés entre les tronçons pérennes et intermittents, et ce quelle que soit la durée d'assèchement. Notamment, dans les tronçons soumis à de sévères assèchements, les communautés étaient, 19 jours après la remise en eau, similaires à celles observées dans les tronçons pérennes. Ces résultats indiquent une résilience exceptionnelle des communautés d'invertébrés dans les rivières alluviales et ont de nombreuses implications en termes de gestion et de prédiction des effets du changement global sur la biodiversité aquatique. Le régime très perturbé de ces rivières sélectionne vraisemblablement des espèces résistantes et résilientes, augmentant ainsi la résilience des communautés. Toutefois, il est fort probable qu'il existe d'autres explications complémentaires, et notamment la présence de refuges lors des assèchements. Dans ces systèmes alluviaux, la zone hyporhéique (sédiments saturés en eau sous le lit de la rivière) est notamment très développée et accessible. Il est fort possible que cette zone soit une source de colonisateurs lors des remises en eau.

Chapitre 4: Est-ce que la dérive est le principal processus permettant la résilience des communautés d'invertébrés aquatiques? Une expérience de terrain dans une rivière alluviale et intermittente.
La dérive a longtemps été considérée comme le processus principal permettant la résilience des communautés. Dans cette étude, j'ai testé cette hypothèse dans une rivière alluviale intermittente par des expériences in situ, notamment pour explorer l'idée que la zone hyporhéique pourrait être une source majeure de colonisateurs. Six chenaux ont été totalement asséchés pendant 1 semaine, tandis que 3 autres (contrôles) ont été laissés en eau. Puis, les chenaux ont été remis en eau pendant 4 semaines, en retenant (n=3) ou non (n=3) les flux d'organismes issus de la dérive. La structure des communautés, leur composition et leur fonction ont été comparées entre les traitements, et le potentiel de colonisation par la dérive, la zone hyporhéique, l'oviposition et la capacité de résistance à la dessiccation ont été quantifiés. J'ai trouvé que les communautés recolonisaient tous les sites après deux semaines de remise en eau, confirmant la forte résilience de ces dernières dans les systèmes alluviaux intermittents. Contrairement à mes hypothèses, la structure des communautés d'invertébrés, leur composition et leur traits fonctionnels n'étaient pas modifiés que la dérive soit bloquée ou non. Ces résultats indiquent que la dérive n'était pas le processus principal permettant la résilience des communautés dans cette rivière. Au contraire, les résultats suggèrent que la zone hyporhéique est la principale source de recolonisation expliquant la forte résilience des communautés. Par conséquent, le rôle de la zone hyporhéique dans la résilience des communautés doit être considéré comme essentiel par les gestionnaires face l'augmentation des pressions provenant du changement climatique et de l'altération des débits. Toutefois, les facteurs environnementaux stimulant l'utilisation de la zone hyporhéique par les invertébrés dans les rivières intermittentes restent méconnus.

Chapitre 5: *Gammarus pulex* (crustacés: amphipodes) évite les fortes températures de l'eau et la compétition en migrant dans la zone hyporhéique: une expérience en mésocosmes.
Avant la disparition complète d'eau en surface, durant les phases initiales de l'asséchement, la température de l'eau peut dépasser les seuils physiologiques de tolérance de nombreuses espèces. De plus, la réduction de la taille de l'écosystème conduit à une concentration des organismes, résultant en une compétition intra et interspécifique très élevée. Pour tester l'influence respective de ces deux facteurs sur la migration des organismes dans la zone hyporhéique, j'ai utilisé 36 mésocosmes consistant en des colonnes de PVC recréant ce qui se produit dans une rivière alluviale qui s'assèche, tout en conservant une zone hyporhéique avec des températures plus faibles. J'ai testé les hypothèses suivantes i) *Gammarus pulex* migre dans la zone hyporhéique afin d'éviter l'augmentation de la température en surface et la compétition intraspécifique, ii) la migration aurait des conséquences négatives sur la survie, sur la consommation de feuilles et sur la réserve énergétique des organismes, iii) ces deux facteurs sont synergiques. L'augmentation de la température à 25°C ainsi que l'augmentation de la densité par 3 entrainent une migration de *G. pulex* dans la zone hyporhéique. De même, la survie, la consommation de feuilles et la réserve en glycogène ont été réduites dans les traitements à haute température et densité, indiquant la présence d'un compromis entre des conditions de surfaces difficiles et un environnent hyporhéique contraint. En revanche, l'interaction des deux facteurs ne semble pas synergique, la compétition n'étant pas plus forte que prévue à hautes températures. Cette étude montre que les invertébrés évitent les températures supérieures à 20°C et la compétition intraspécifique en utilisant la zone hyporhéique comme refuge. Ces résultats ont des implications importantes dans un contexte de changement climatique entraînant des hausses de température et l'asséchement accru des cours d'eau. Il reste toutefois à déterminer comment la capacité de la zone hyporhéique à servir de refuge évolue dans le temps, puisque son utilisation a un coût physiologique.

Chapitre 6: La profondeur de la zone hyporhéique pendant l'assèchement de la rivière influence la résilience de *Gammarus pulex* et altère le fonctionnement de l'écosystème.
Comme indiqués dans les précédents chapitres, les migrations verticales des invertébrés dans la zone hyporhéique favorisent la résilience des communautés. Cependant, les facteurs limitant ces mouvements, comme la profondeur de la zone hyporhéique, sont relativement peu connus. J'ai testé en mésocosmes comment la résilience de *Gammarus pulex*, mesurée par la survie et le % d'individus retournés à la surface (% RTS), était affectée par un asséchement d'une semaine avec différentes profondeurs de zone hyporhéique (contrôle, −5 cm, −30 cm, à sec). J'ai mesuré la décomposition des feuilles en surface afin d'évaluer les effets du niveau de l'eau sur le fonctionnement de l'écosystème et les réserves en glycogène des organismes afin d'estimer le coût énergétique associés à la migration dans la zone hyporhéique. Deux populations, provenant de rivières intermittentes et pérennes, ont été testés afin d'évaluer la variabilité inter-population de la réponse aux asséchements et la potentiel adaptation locale. La survie et % RTS ont été respectivement réduits jusqu'à 39 et 52%, dans les

traitements −30 cm et à sec, induisant des effets en cascade sur la décomposition des feuilles, qui a été réduite jusqu'à 46%. Une forte variabilité inter-populations est mesurée concernant le % RTS, mais en général, peu de différences ont été observées sur la survie et la décomposition des feuilles. Mes résultats suggèrent que des variations, même faible, de la profondeur de la zone hyporhéique lors d'assèchements, pourraient réduire la résilience et entraîner des effets en cascade sur le fonctionnement des écosystèmes en diminuant le rôle de la zone hyporhéique comme source de colonisation dans les rivières intermittentes. Ces résultats préconisent une gestion accrue de la zone hyporhéique, notamment dans les systèmes où celle-ci est menacée par les prélèvements en eau dans la nappe.

Dans cette thèse, j'ai montré que les asséchements n'ont pas toujours des effets sévères sur les communautés d'invertébrés des rivières alluviales qui semblent très résilientes. Cette résilience est en partie due au filtrage des espèces du pool régional et la co-tolérance à de multiples perturbations naturelles. Ceci implique de bien considérer les régimes de perturbations actuels et historiques afin d'affiner les prédictions des effets des assèchements des cours d'eau sur leur biodiversité et leur fonctionnement écologique. D'autre part, dans ces rivières alluviales, la zone hyporhéique peut constituer une source d'invertébrés jouant un rôle primordial dans la résilience des communautés. A la manière de banques de graines, ces « réserves » d'organismes favorisent la persistance des communautés, diminuent les risques d'extinction locale, permettent la coexistence d'espèces compétitrices et influencent la structure génétique des populations et communautés. Cependant, l'utilisation de la zone hyporhéique par les organismes a sans doute des limites puisqu'elle a un cout physiologique. En termes de gestion, l'accent devrait être mis sur la préservation de l'existence et de l'accessibilité de la zone hyporhéique dans les rivières alluviales afin de préserver cette capacité de résilience face aux changements globaux.

De futures travaux pourraient généraliser ces résultats en explorant comment la résilience des communautés est affectée par les perturbations sur différents types d'écosystèmes présentant des gradients de perturbations. Il sera également important de quantifier les effets de la compétition interspécifique en conditions environnementales de surface stables ou sévères afin de comprendre le rôle de « storage effect » de la zone hyporheique, notamment sur la coexistence des espèces. De plus en plus de rivières autrefois pérennes s'assèchent, d'où l'intérêt de mener des études permettant de tester les impacts de l'assèchement sur la résistance à la dessiccation, la tolérance thermique et le comportement de migration verticale et cela avec des peuplements provenant de cours d'eau intermittents et pérennes. Cela permettra de tester si les organismes de populations de milieux pérennes ont acquis les mêmes adaptations physiologiques et comportementales que ceux des populations de rivières naturellement intermittentes. Enfin, en termes de gestion, il apparait essentiel de localiser à large échelle les tronçons de rivières où la zone hyporhéique pourrait jouer un rôle majeur dans la résilience des communautés en développant un outil de gestion basé sur la

géomorphologie (*i.e.* tronçons contraints vs plaines alluviales, dépôts sédimentaires, taille du substrat), l'hydrologie (*i.e.* profondeur de la zone hyporhéique) et l'occupation de sol (*i.e.* % sol cultivés, prélèvements dans la nappe, risque de colmatage des sédiments).

Forward

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List of articles published or submitted

Included in this thesis

Vander Vorste, R. F. Mermillod-Blondin, F. Hervant, R. Mons and T. Datry. *Gammarus pulex* avoids both increasing water temperature and intraspecific competition through vertical migration into the hyporheic zone: results from a mesocosm experiment. Aquatic Sciences. Accepted Dec. 2015.

Vander Vorste, R. F. Mermillod-Blondin, F. Hervant, R. Mons and T. Datry. Increased depth to the water table during river drying decreases the resilience of *Gammarus pulex* and alters ecosystem function. Ecohydrology. Accepted Dec. 2015.

Vander Vorste, R., R. Corti, A. Sagouis, and T. Datry. 2015. Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. Freshwater Science: doi:10.1086/683274.

Vander Vorste, R., F. Malard, and T. Datry. 2015. Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an alluvial, intermittent river. Freshwater Biology: doi:10.1111/fwb.12658.

Not included in this thesis

Leigh, C., N. Bonada, A. Boulton, B. Hugueny, S.T. Larned, R. Vander Vorste, and T. Datry. In press. Invertebrate assemblage responses and the dual roles of resistance and resilience to drying in intermittent rivers. Aquatic Sciences: doi: 10.1007/s00027-015-0427-2.

Conference Presentations

Vander Vorste, R., F. Mermillod-Blondin, F. Malard, and T. Datry. 2015. The hyporheic zone as a primary source of resilience for invertebrate communities in intermittent alluvial rivers: evidence from field and laboratory studies. Society for European Freshwater Science Biannual Conference. Geneva, CH.

Vander Vorste, R., F. Mermillod-Blondin, F. Malard, and T. Datry. 2015. The hyporheic zone as a primary source of resilience for invertebrate communities in intermittent alluvial rivers: evidence from field and laboratory studies. Society for Freshwater Science Annual Conference. Milwaukee, WI.

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Chapter 1:
Introduction & Objectives

Chapter 1: Introduction and Objectives

1.1 Community assembly and the role of disturbance in aquatic ecosystems

1.1.1 Processes that determine community assembly

One pervasive goal of community ecology is to identify the processes that determine community assembly, as measured by community richness, abundances and composition, at spatiotemporal scales of interest (Leibold *et al.* 2004, Vellend 2010, Heino *et al.* 2015). At broad scales (*e.g.* continents), evolutionary processes (*e.g.* speciation), climate (*e.g.* temperature regime), historical events (*e.g.* glaciation) and dispersal (*e.g.* flight) act together to determine a regional species pool (Tonn 1990, Poff 1997, Mykrä *et al.* 2007; Figure 1.1). From the regional species pool, a series of selective abiotic (*e.g.* substrate type) and biotic filters (*e.g.* competition) operating over multiple, nested habitat levels (*e.g.* catchment, river reach, riffle) further constrain species and form local communities (Poff 1997, Lamouroux *et al.* 2004, Thompson and Townsend 2006; Figure 1.1). In this regard, community assembly is a deterministic process in which environmental conditions have a key role in species distribution (*i.e.* niche model; Whittaker *et al.* 1973, Chase and Leibold 2003).

However, stochastic processes such as colonization, births, deaths and random changes in species relative abundances (*i.e.* ecological drift) are also of considerable importance in community assembly (*i.e.* neutral model, Hubbell 2001, Chase and Myers 2011, Zhou *et al.* 2014). Contrary to the niche model, the neutral model insists that local community composition cannot be predicted by local environmental conditions alone and highlights the potential importance of rare or random events (*e.g.* passive dispersal). Here, organisms are assumed to be identical in their probabilities of migration, births, deaths and speciating (Hubbell 2001). These assumptions help explain how high site-to-site variation in species composition can occur between locations (*e.g.* headwater streams) with similar environmental conditions (*e.g.* Clarke *et al.* 2010, Finn *et al.* 2013). In reality, both deterministic and stochastic processes are likely to occur (Leibold *et al.* 2004, Vellend 2010, Heino *et al.* 2015) and this realization has made disentangling the importance of these two processes a burgeoning field of ecology (Siepielski *et al.* 2010, Chase and Myers 2011, Vellend *et al.* 2014).

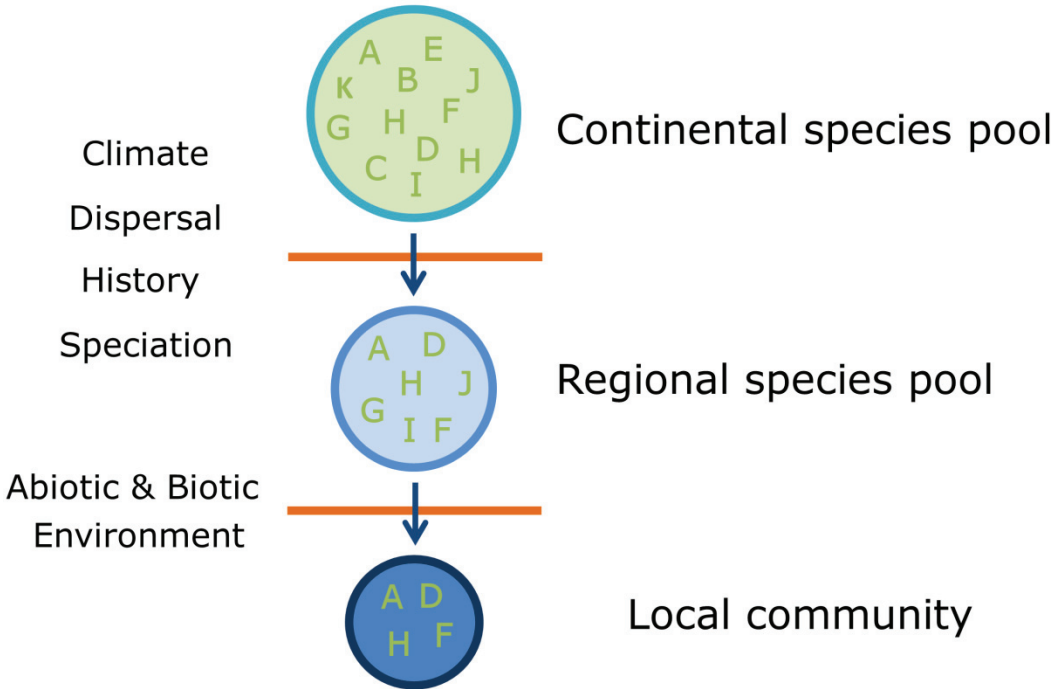

Figure 1.1 Multiple filters operating on species (A–K) at hierarchical scales which form a local community in aquatic ecosystems (*e.g.* rivers). Adapted from Poff (1997).

Current research on the relative roles of deterministic and stochastic processes in community assembly have emphasized that the importance of these processes can change across environmental (*e.g.* disturbance, productivity, biotic interactions) and spatial (*e.g.* elevation, latitude) gradients (Chase and Myers 2011, Kraft *et al.* 2011 Heino *et al.* 2015). In particular, disturbances may influence community assembly in aquatic ecosystems (*e.g.* Chase 2007, Zhou *et al.* 2014). Indeed, aquatic ecosystems are subjected to a myriad of natural and anthropogenic disturbances (Dudgeon *et al.* 2006, Malmqvist *et al.* 2008) and research into the effects of disturbances on aquatic communities is a major research priority (Woodward *et al.* 2010, Hawkins *et al.* 2015), especially following growing recognition that climate change and other anthropogenic pressures will exacerbate disturbances, such as floods and droughts (Thompson *et al.* 2013, Jaeger *et al.* 2014).

1.1.2 Importance of disturbance to community assembly in aquatic ecosystems

Disturbances are a major element of community assembly because they can shift the relative importance of deterministic and stochastic processes (Chase 2007, Zhou *et al.* 2014). They are a physical force, agent or process, either abiotic or biotic, that cause a response (*e.g.* mortality) in the constituent species, populations or communities (*sensu* Rykiel 1985). On one hand, the harsh abiotic and biotic factors associated with disturbances are predicted to further filter the regional species pool by allowing only disturbance-tolerant species to colonize, essentially increasing the relative importance of deterministic processes (Chase 2007, Lepori and Malmqvist 2009, Kraft *et al.* 2015;

Figure 1.2). Indeed, in many aquatic ecosystems, both natural and anthropogenic disturbances can lower richness and alter community composition and abundance (Resh *et al.* 1988, Altermatt *et al.* 2011, Hawkins *et al.* 2015). On the other hand, discrete disturbance events (*e.g.* flooding, drying) open space or other resources (Sousa 1984), encouraging colonization, which, for many aquatic organisms, is considered to be a stochastic processes in regards to when and what order species will arrive (Belyea and Lancaster 1999, Lowe and McPeek 2014, Heino *et al.* 2015; Figure 1.2). These dichotomous perspectives underline why understanding the response of communities to disturbance and the subsequent colonization is an essential part of identifying the processes that determine community assembly (Lake 2000, Mackey and Currie 2001, Huston 2014).

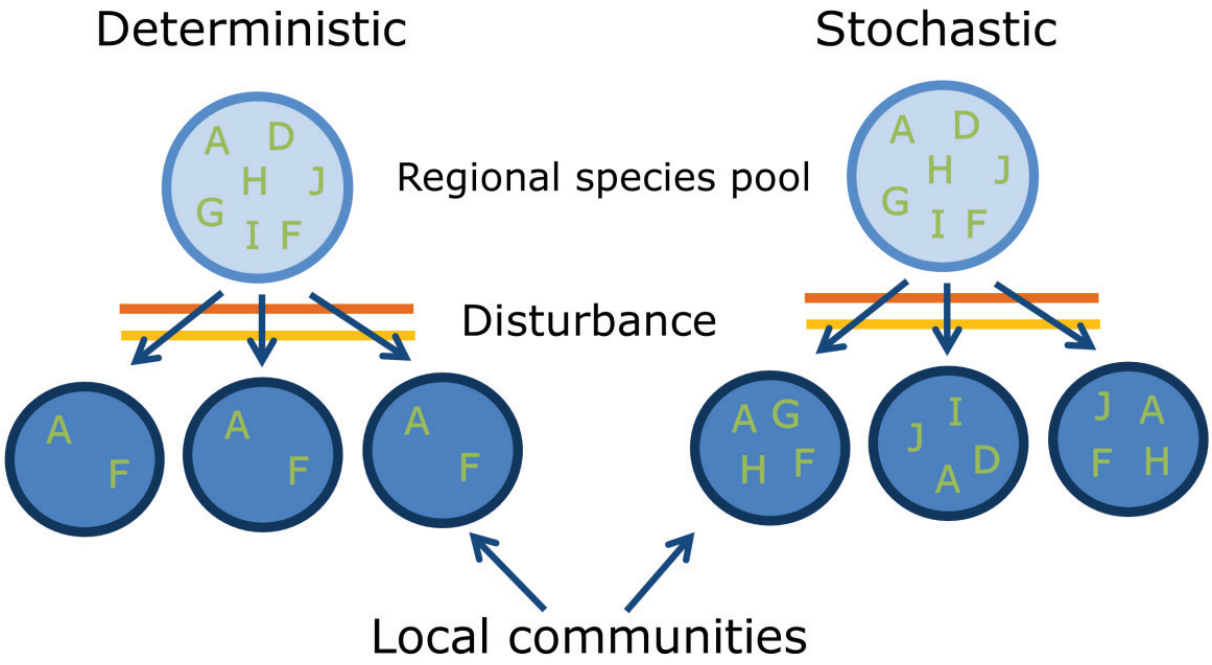

Figure 1.2 Dual perspectives, deterministic or stochastic, regarding the effects of disturbances on community assembly processes.

There is considerable uncertainty surrounding the effects of disturbances on communities and subsequent colonization of previously disturbed habitats in aquatic ecosystems (Ives and Carpenter 2007, Stanley *et al.* 2010, Darling *et al.* 2013). For example, the intermediate disturbance hypothesis, which has served a predominate role in disturbance ecology, argues that diversity at local spatial scales is highest at moderate levels of disturbance frequency and/or intensity (Connell 1978). However, there is a paucity of empirical, observational or theoretical support for this relationship (Mackey and Currie 2001, Randall Hughes *et al.* 2007, Fox 2013). Furthermore, the fact the most communities now face multiple natural and/or anthropogenic disturbances simultaneously or consecutively have made testing the effects of one disturbance across a gradient of frequency/intensity virtually impossible or irrelevant without considering the legacies of prior of disturbances and initial community composition

(Vinebrooke *et al.* 2004, Côté and Darling 2010, Buma 2015). To overcome this, ecologists have been urged to consider how disturbances affect communities across different types of ecosystems that may be more or less susceptible based on prior history of disturbances (Peters *et al.* 2011, Chase and Knight 2013, Buma 2015).

The subsequent colonization following disturbance (*i.e.* succession; Connell and Slatyer 1977) controls the magnitude and direction of community response (Sousa 1980, Lake 2000, Zhou *et al.* 2014), yet this process is not well quantified in many aquatic ecosystems (Lake *et al.* 2007, Prach and Walker 2011). To better understand community succession, research has begun to focus on processes that promote community resilience following a disturbance (*i.e.* the capacity to recover to levels similar pre-disturbance conditions or those in undisturbed sites; Stanley et al. 1994, Bogan *et al.* 2014, Datry et al. 2014). Considering not all members within a community will resist disturbance *in situ*, it is crucial to identify and quantify the sources that provide colonists and promote resilience following disturbance (Ashcroft 2010, Hannah *et al.* 2014, Keppel *et al.* 2015). However, quantification of sources that drive community resilience has rarely been performed at scales that are relevant to the disturbances being studied (Englund and Cooper 2003, Prach and Walker 2011, Olden *et al.* 2014).

1.1.3 Global climate change and water abstraction: realized and future impacts on aquatic ecosystems

Global climate change and other anthropogenic pressures are a major threat to biodiversity (*i.e.* the number and relative abundance of species, Pielou 1977) and ecosystem functions (*i.e.* the production, decomposition and elemental cycling that determine energy and material flows through a system; Schmitz *et al.* 2008) in aquatic ecosystems (Parmesan and Yohe 2003, Dudgeon *et al.* 2006, Jeppesen *et al.* 2015). Climate change impacts aquatic ecosystems through increased water temperature (Kaushal *et al.* 2010) and alteration of precipitation (Trenberth 2011) and runoff patterns (van Vliet *et al.* 2013). These changes are superimposed over increased anthropogenic pressures that have resulted in river flow modification, habitat degradation, water pollution, abstraction and species invasion (Dudgeon *et al.* 2006, Strayer and Dudgeon 2010). Together, the effects of climate change and other anthropogenic pressures on aquatic ecosystems have been attributed to large declines in biodiversity and ecosystem functions (Dudgeon *et al.* 2006, Hoegh-Guldberg and Bruno 2010, Burkhead 2012, Vaughn *et al.* 2015). Among the organisms affected, aquatic invertebrates–a ubiquitous group involved in key ecosystem functions–appear particularly susceptible to climate change and anthropogenic pressures because of their ectothermic physiologies and limited ability to track favorable environmental conditions (Lancaster and Briers 2008, Isaak and Rieman 2013, Vaughn *et al.* 2015). Therefore, further increases in water temperature and river flow modification are predicted to

have strong negative consequences on aquatic invertebrates and the ecosystem functions they perform (*e.g.* organic matter decomposition; Fagan 2002, Kishi *et al.* 2005, Handa *et al.* 2014).

Future increases in water temperature, water abstraction and alteration of river flow regimes pose one of the greatest threats to aquatic biodiversity and ecosystem functions (Poff *et al.* 2007, Woodward *et al.* 2010). Within the next century, mean water temperature is expected to increase by an additional 0.8–1.6°C globally (van Vliet *et al.* 2013). Extreme high temperatures are also expected to increase in intensity (*i.e.* maximum), frequency and duration above current climatic conditions (Easterling *et al.* 2000, Jentsch *et al.* 2007, Mantua *et al.* 2010). These increases in mean and extreme temperatures will likely have physiological, ecological and evolutionary consequences on aquatic invertebrates (Jentsch *et al.* 2007, Kreyling *et al.* 2011, Thompson *et al.* 2013). Furthermore, increased water abstraction will continue to alter the flow regime, or hydroperiod, of freshwater rivers, lakes and wetlands at a global scale (Baron *et al.* 2002, Palmer *et al.* 2008, Jeppesen *et al.* 2015). Decreases in water availability between 10–30% in southern Africa, southern Europe, the Middle-East and mid-latitude western North America by the year 2050 (Milly *et al.* 2005) will amount to more frequent and longer periods of surface water drying in these regions (Datry *et al.* 2014, Jaeger *et al.* 2014, Jeppesen *et al.* 2015). The abiotic and biotic effects of increased frequency and duration of surface water drying on aquatic invertebrate communities must be quantified before predictions about the global-scale influence of climate change and other related anthropogenic pressures on biodiversity and ecosystem functions can be addressed (Larned *et al.* 2010, Vaughn 2010).

1.2 Surface water drying as a fundamental driver of aquatic communities

1.2.1 Progression of surface water drying on aquatic habitats

Surface water drying involves a progression through identifiable thresholds beginning with the initial contraction of aquatic habitat from the littoral vegetation up to the eventual drying of the hyporheic zone (*i.e.* the saturated sediments below and adjacent to the riverbed; White 1993; Figure 1.3). Described as a ramp disturbance because there is a steady increase in harshness over time (Lake 2000), drying begins with the contraction of aquatic habitat area (Figure 1.3a) that can eventually lead to fragmentation when the shallow aquatic habitats (*e.g.* riffles) dry and leave only deeper habitats (*e.g.* pools) with surface water (Figure 1.3b; Stanley *et al.* 1997). In lotic systems, flow gradually decreases until complete cessation occurs when habitats become fragmented (Dewson *et al.* 2007). Next, contraction of isolated pools continues until eventually all surface water dries (Figure 1.3c) unless spring-fed water sources, which generally flow permanently, are available (Lake 2000). Prolonged drying will increase the depth to the saturated sediments in the hyporheic zone (*i.e.* water table depth; Boulton 2003; Figure 1.3d).

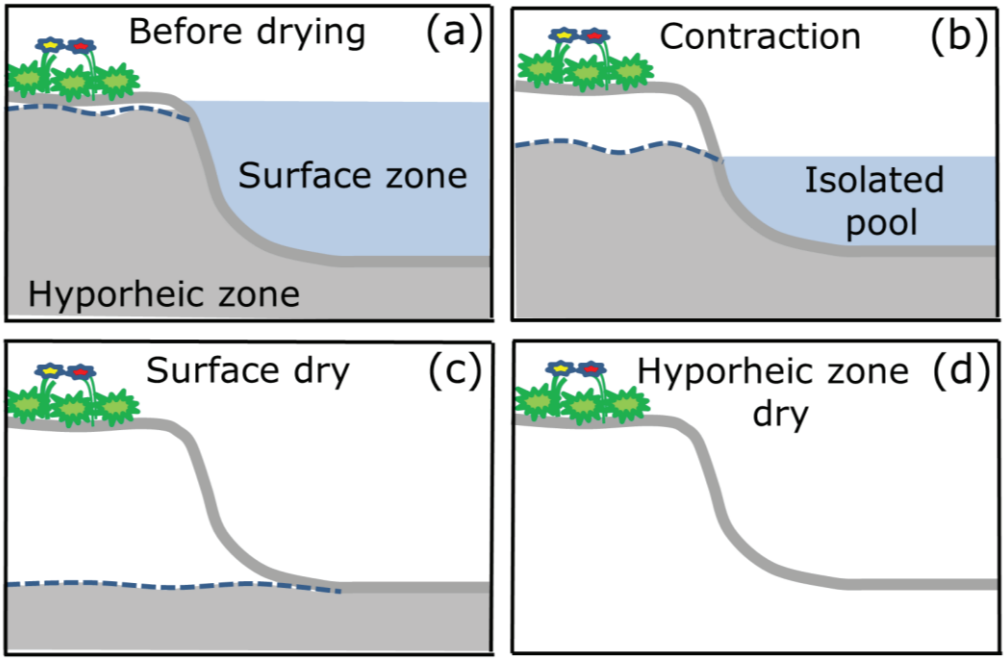

Figure 1.3 Cross-sectional diagram of river or pond system (a) showing progression through drying phases from the initial contraction phase (b), to complete surface drying (c) and finally drying of the hyporheic zone (d).

1.2.2 Abiotic and biotic factors associated with surface water drying and their effects on aquatic invertebrates

Along the progression of drying, abiotic and biotic environmental factors often become increasingly harsh for aquatic invertebrates (Bonada *et al.* 2006, Dewson *et al.* 2007, Rolls *et al.* 2012). The initial decrease of flow in lotic systems and water level in ponds generally coincides with lower dissolved oxygen and increased sedimentation (Wood and Armitage 1999, Dewson *et al.* 2007). These changes, in turn, drive a loss of rheophilic (most Ephemeroptera, Plecoptera and Trichoptera) and filter-feeding taxa (*e.g.* Simuliidae, Hydropsychidae) that require flowing water to persist or are sensitive to fine sediments (Bonada *et al.* 2006, Dewson *et al.* 2007). As aquatic habitats contract further, surface water temperature can increase to levels above 25°C in drying river pools (Ludlam and Magoulick 2010) and 40°C in drying ponds (Williams 2006). Insect larvae (*e.g.* Ephemeroptera, Plecoptera, Trichoptera), and crustaceans (*e.g.* Amphipoda, Isopoda) experience drastic increases in mortality between 21–25°C (Stewart *et al.* 2013a, Foucreau *et al.* 2014). In addition, habitat contraction can lead to increases in species density and subsequently higher intra- and interspecific competition for space and food (Lake 2003). For example, Covich *et al.* (2003) measured a two to three-fold increase in mean densities of some species (*e.g.* freshwater shrimp (Crustacea: Decapoda) in pools of a drying tropical river.

Once pools dry, environmental conditions become harsher and further constrain aquatic invertebrates (Williams 1996, Boulton 2003, Lake 2003). For example, dry riverbeds can reach extreme

temperatures, especially in Mediterranean and arid-land climates (e.g. > 60°C; Boulton *et al.* 1992, Gasith and Resh 1999). At this point, only taxa with desiccation resistance forms may remain on the channel surface (Stubbington and Datry 2013). Whereas, some taxa may continue to follow the water table into the hyporheic zone as drying progresses, up to depths of 1 m (*e.g.* Clinton *et al.* 1996).

1.2.3 Long-term effects of surface water drying on aquatic invertebrate communities

Drying is considered a major driver of aquatic invertebrate communities because it can induce declines in taxonomic richness that persist for several months to years (Wellborn *et al.* 1996, Lake 2003, Williams 2006, Datry *et al.* 2014). These effects appear to be most directly related to the duration of drying, rather than frequency of drying events (but see Ledger *et al.* 2012), where communities in rivers and ponds without surface water for much of the year have low richness and are dominated by a small pool of ubiquitous taxa (Wellborn *et al.* 1996, Vanschoenwinkel *et al.* 2010, Datry *et al.* 2014). Across 14 rivers in Europe, North America and New Zealand, Datry *et al.* (2014) found taxonomic richness decreased linearly along an annual flow intermittence gradient (*i.e.* duration of the year when surface water is lost). Similarly in ponds, invertebrate communities showed a negative relationship between species richness and duration of surface water drying (Vanschoenwinkel *et al.* 2010). Despite these generalities, very few studies have examined if similar effects of drying on communities occur in aquatic ecosystems along other environmental (*e.g.* climate, productivity) or spatial (*e.g.* elevation, latitude) gradients. Considering these gradients can have a strong influence on the regional species pool (Southwood 1988, Heino 2011), some communities may be more or less affected by drying than others because of inherent physiological, morphological and life-history traits of the constituent species that could promote their resistance or resilience (Vinebrooke *et al.* 2004, Bonada *et al.* 2007, Bogan *et al.* 2014).

1.3 Resistance and resilience of aquatic invertebrate communities to surface water drying

1.3.1 Traits of aquatic invertebrates that promote resistance and resilience

The effects of surface water drying on aquatic invertebrate communities depend on the resistance and resilience of constituent taxa (Stanley *et al.* 1994, Fritz and Dodds 2004, Bogan *et al.* 2014). Traits related to the physiological, morphological and life-history features of an organism are frequently used to confer resistance and resilience of species to disturbance (Lepori and Hjerdt 2006, Bonada *et al.* 2007, Verberk *et al.* 2013). Resistance can be defined as the capacity of a taxon, a community, or an ecosystem to persist unchanged through a disturbance (Stanley *et al.* 1994, Bogan *et al.* 2014, Datry *et al.* 2014). For aquatic invertebrates, traits that allow *in situ* desiccation-resistance include: diapause, desiccation-resistant eggs, cocoons or cells, body armoring and aerial respiration (Bonada *et al.* 2007,

Robson *et al.* 2011, Boersma and Lytle 2014; Figure 1.4). Whereas, traits that enhance the resilience of invertebrates to drying by either fast reproduction/growth rates or high dispersal ability include: small body-size (≤ 9 mm), asexual reproduction, active aerial dispersion and swimmer habit (Bonada *et al.* 2007, Datry *et al.* 2014; Figure 1.4). Inherently, taxa that resist disturbance also contribute to resilience but, in general, few aquatic invertebrates are able to resist complete drying (Lake 2003, Robson *et al.* 2011, Bogan *et al.* 2014). Therefore, persistence of aquatic communities in systems that experience drying is mainly driven by the various processes of colonization from nearby or distant sources (Robson *et al.* 2013, Bogan *et al.* 2014, Datry *et al.* 2014).

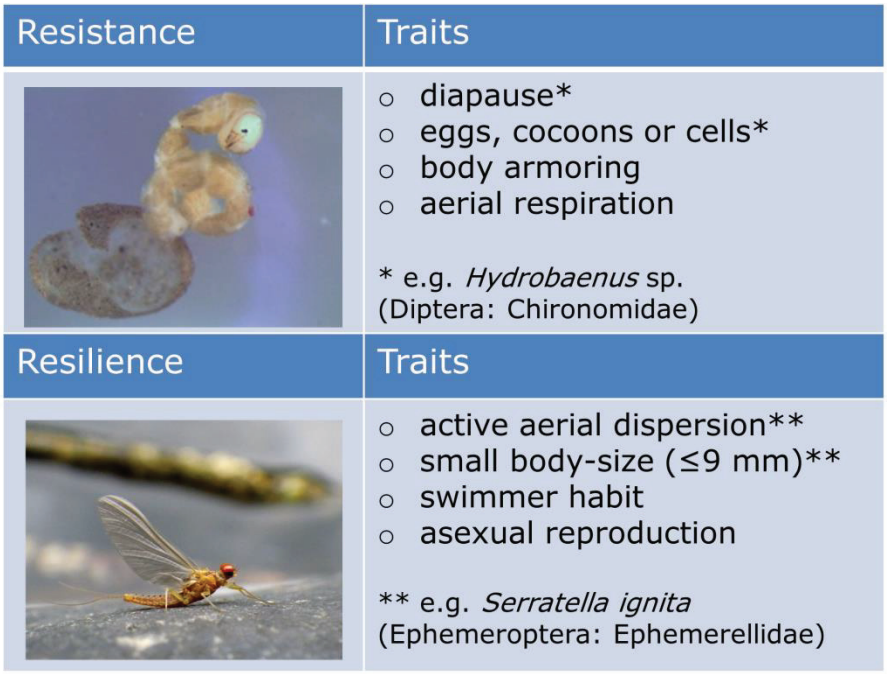

Figure 1.4 Examples of traits that enhance the resistance and resilience of aquatic invertebrates to surface water drying**.**

1.3.2 Processes promoting colonization of previously dry habitats

There are three primary processes, occurring longitudinally, laterally and vertically, that invertebrates use to colonize previously dry habitats in rivers; drift, aerial colonization or oviposition and vertical migration (Williams and Hynes 1976, Lake 2000, Chester and Robson 2011; Figure 1.5). Of these processes, drift (*i.e.* the active or passive downstream transport of organisms; Bilton *et al.* 2001) is considered the most important process of colonization due to the unidirectional movement of water from upstream to downstream. However, the number of studies investigating the abiotic and biotic causes of drift overwhelm those that quantify its importance to colonization following disturbances, such as drying (Müller 1954, Townsend and Hildrew 1976, Kennedy *et al.* 2014). Aerial colonization from nearby and distant sources (*e.g.* perennial rivers) and vertical migration from the hyporheic zone

may also be important sources, especially in systems where upstream sources of drift are not available (*e.g.* intermittent headwater streams). This recognition highlights the importance of quantifying the relative contribution of the different sources of colonization in order to understand community resilience to drying across aquatic ecosystems.

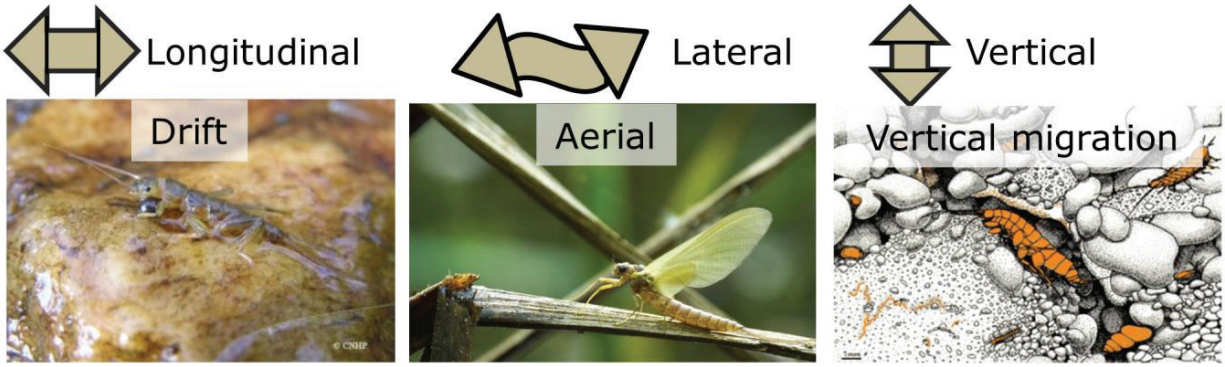

Figure 1.5 Primary processes of colonization following surface water drying events occurring longitudinally (*e.g.* drift), laterally (*e.g.* aerial) and vertically (*e.g.* vertical migration), representing three dimensions.

1.4 Hyporheic zone as a source of colonization following surface water drying

1.4.1 The hyporheic zone

The hyporheic zone is an interface between surface water and the groundwater aquifer where water, nutrients, organic matter and biota are exchanged (Boulton *et al.* 1998). In rivers with high substrate permeability, the hyporheic zone can be an important habitat for hydrological, biogeochemical and ecological processes that extends vertically (up to 10 m) and laterally (up to 2 km) from the main river channel (*e.g.* Stanford and Ward 1988). Conversely, the vertical and lateral extent of the hyporheic zone can be greatly reduced in rivers with low substrate permeability (Vervier *et al.* 1992). Furthermore, the direction and magnitude of surface-subsurface water exchange (*i.e.* exchange flow) can also greatly influence how the hyporheic zone interacts with the surface and groundwater (Boulton *et al.* 1998). For example, when water upwells from the hyporheic zone to the surface, due to the geomorphological or bed-form features of the river, it can increase nutrient levels and lower surface water temperature during summer months (Doering *et al.* 2013, Capderrey *et al.* 2013); whereas, when surface water downwells into the hyporheic zone, a significant amount of nutrients and organic matter may be stored (Valett *et al.* 1990, Findlay 1995).

1.4.2 Evidence of hyporheic zone use by invertebrates during disturbances

Colonization of the hyporheic zone by benthic invertebrates was first reported over 60 years ago (Angelier 1953, Orghidan 1955). It has since been recognized as a potential refuge (*i.e.* providing protection from disturbances or advantages in biotic interactions, such as competition or predation; Keppel *et al.* 2012) for benthic invertebrates (*i.e.* hyporheic zone refuge hypothesis; Williams and Hynes 1974, Palmer *et al.* 1992, Dole-Olivier 2011). However, strong empirical evidence supporting the hyporheic refuge hypothesis has not been forthcoming, especially in regards to stream drying (Dole-Olivier 2011). Indeed, invertebrate use of the hyporheic zone depends greatly on its physical properties and spatial organization which limit its accessibility to invertebrates (Dole-Olivier 2011, Stubbington 2012). For instance, the proportion of fine sediments (< 2 mm), porosity and hydraulic conductivity control the vertical migration of invertebrates (Navel *et al.* 2010, Descloux *et al.* 2014, Vadher *et al.* 2015). Furthermore, the direction of exchange flow can facilitate or impede vertical migration depending, respectively, on its downwelling or upwelling direction (Dole-Olivier *et al.* 1997, Olsen and Townsend 2003, Mathers *et al.* 2014). Although several studies have measured increased abundance of benthic invertebrates in the hyporheic zone during drying events (*e.g.* Clinton *et al.* 1996, Wood *et al.* 2010, Stubbington *et al.* 2015), this supporting evidence is not consistent across all studies (*e.g.* del Rosario and Resh 2000, James *et al.* 2008). Furthermore, it is still questioned if the hyporheic zone serves as a source of colonization following disturbance or if it is a 'graveyard' for benthic invertebrates (Dole-Olivier 2011).

The distinction between the hyporheic zone as a source of colonization or a 'graveyard' has strong implications for persistence of communities following disturbances. For example, disturbances reduce the recruitment (*i.e.* birth and immigration) of species by significantly lowering their densities, and this can have long-term effects on diversity and ecosystem functions unless recruitment (colonization) can occur from organisms that survived the disturbance (*i.e.* storage effect; Chesson and Warner 1981, Warner and Chesson 1985). Such could be the case in rivers experiencing drying, where the significant reduction in richness and density of benthic invertebrates on the surface can be mitigated if adequate colonization from organisms that survived in the hyporheic zone occurs. Furthermore, the storage effect generated by those surviving organisms can be responsible for the coexistence of competing species (Warner and Chesson 1985, Cáceres 1997, Angert *et al.* 2009). This occurs if a competitively inferior species has higher survival and therefore higher recruitment following disturbances compared to its competitively superior counterpart (*e.g.* Cáceres 1997). Therefore, there are important ecological implications regarding the potential of the hyporheic zone to be a source of colonization following drying and quantifying this potential could improve our understanding of community assembly in aquatic ecosystems.

1.4.3 Knowledge gaps regarding the hyporheic zone as a source of colonization

Determining the importance of the hyporheic zone as a source of colonization has been hindered by a lack of empirical evidence that (i) quantifies its role relative to other potential sources of colonization (*i.e.* drift, aerial oviposition, resistance forms), (ii) identifies what environmental factors influence vertical migration and (iii) explores how resilience of invertebrates and ecosystem functions can be affected by characteristics of the hyporheic zone that limit vertical migration. First, support for the relative importance of the hyporheic zone as a source of colonization has been developed from a few small-scale experiments (*e.g.* < 0.5 m²; Townsend and Hildrew 1976, Williams and Hynes 1976, Fowler 2002, Bruno *et al.* 2012). For example, Williams and Hynes (1976) and Williams (1977) studied the relative importance of colonization sources in three Canadian rivers using several colonization chambers (60 × 30 cm) that allowed colonization from either upstream, downstream, vertical migration from the hyporheic zone or aerial oviposition. These authors reported only limited importance of the hyporheic zone. These small-scale studies, however, have been criticized for their lack of relevancy to large-scale flow disturbances and reach-scale experiments have been urged to better understand the response of communities to disturbances (Englund and Cooper 2003).

Second, outside of the physical substrate characteristics and spatial factors that may influence vertical migration of invertebrates, there is little empirical evidence addressing the environmental factors that may influence invertebrate use of the hyporheic zone. It has been hypothesized that water temperature and competition, which can increase dramatically during drying events, initiate the vertical migration of invertebrates into the hyporheic zone (James *et al.* 2008, Wood *et al.* 2010, Stubbington *et al.* 2011). However, the constant interplay of these two factors and their potential interaction on invertebrates has made their effects difficult to tease apart based on field surveys (Stubbington *et al.* 2011). Therefore, it is unknown at what temperature and levels of competition invertebrates are triggered to vertically migrate from the surface to the hyporheic zone. These potential thresholds are important for identifying when significant changes in biotic communities will occur and are used by ecologists and river managers to predict responses to climate change and set management priorities (Dodds *et al.* 2010).

Third, it is still unknown how physical characteristics of the hyporheic zone that limit vertical migration affect the resilience of invertebrates and the ecosystem functions they perform. The depth to the water table (*i.e.* the thickness of the vadose zone between the streambed surface and the saturated hyporheic zone) is an important factor that can determine whether the hyporheic zone is used as a refuge during drying events (Clinton *et al.* 1996, Boulton *et al.* 1998, Stubbington *et al.* 2011). During drying events, the water table generally remains close to the surface in river reaches with upwelling conditions; whereas, depth to the water table can gradually increase during drying in reaches with downwelling conditions due to loss of surface water via transmission into the substrate (Boulton 2003,

Datry *et al.* 2007, Datry 2012). In the latter case, organisms will be forced to navigate further into the hyporheic zone, increasing their energetic cost and risk of becoming stranded in dry substrate (Shepard *et al.* 2013, Stumpp and Hose 2013). Subsequent mortality will reduce the number of individuals that return to the surface following drying and this may have cascading effects on the ecosystem functions, such as leaf litter decomposition, that these invertebrates perform.

1.5 Alluvial rivers as model systems to study the resilience of invertebrate communities to surface water drying

1.5.1 Alluvial rivers

Alluvial rivers are characterized by single or multiple channels that are self-formed by transport and deposition (*i.e.* cut and fill) of often coarse, mobile sediments across an active floodplain (Church 2006). Because of high substrate porosity, alluvial rivers are typified by the high volume of water (up to 30% at base flow; Poole *et al.* 2006) that flows through interstitial pathways underneath the riverbed (*i.e.* hyporheic corridors; Stanford and Ward 1993). A typical formation of alluvial rivers from source to mouth, includes headwater reaches that are constrained into a single channel, highly unstable, braided (multiple) reaches and finally meandering reaches which again form single channels (Ward and Stanford 1995; Figure 1.6). Along this continuum, the relative importance of surface-subsurface water exchange to hydrological and ecological processes, as opposed to lateral (*e.g.* floodplain) or longitudinal (*e.g.* upstream-downstream), is predicted to peak along braided reaches (Ward and Stanford 1995; Figure 1.6).

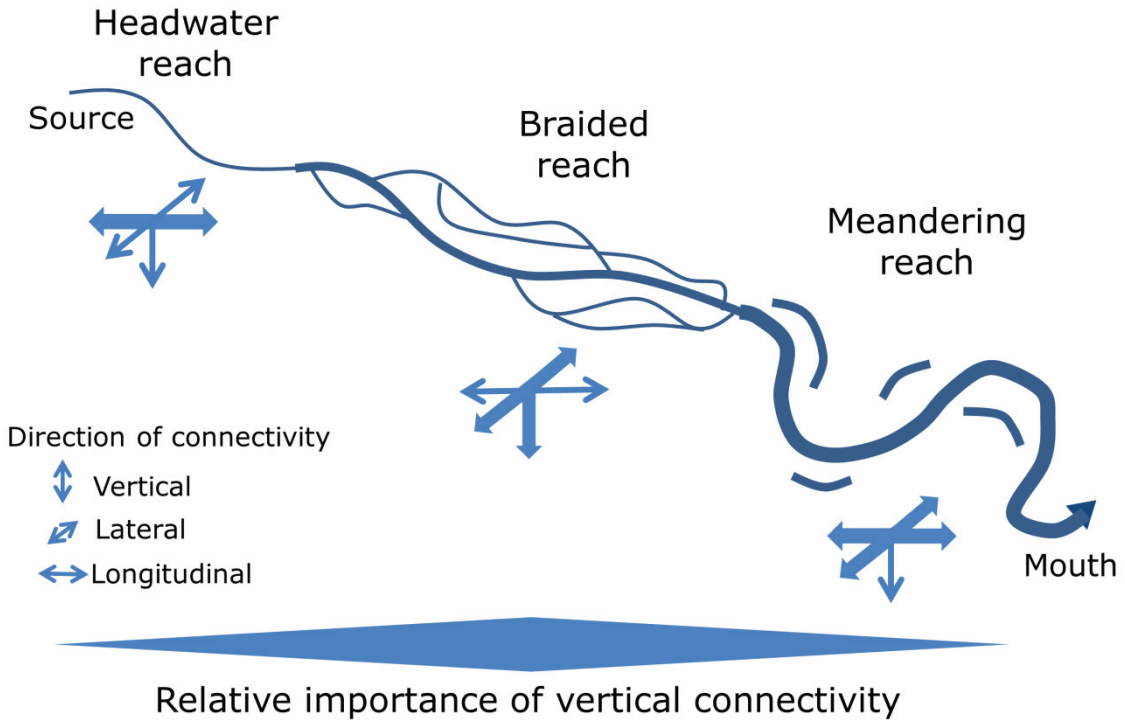

Figure 1.6 Idealized channel pattern of alluvial rivers along a longitudinal gradient from source to mouth. Arrows indicate hypothesized direction of hydrological and ecological connectivity. Thickness of arrows indicates relative importance of connectivity to hydrological and ecological processes (adapted from Ward and Stanford 1995).

Within braided reaches, the vertical direction of surface-subsurface exchange varies longitudinally at multiple scales as determined by the underlying geology and channel features within the system (Stanford and Ward 1993, Malard *et al.* 2003, Poole 2010; Figure 1.7). For example, at large scales (several km), river sections that are bounded and unbounded by valley constrictions (*e.g.* canyons) create upwelling and downwelling zones of vertical exchange flows, respectively (Stanford and Ward 1993; Figure 1.7). At smaller scales (< 100m), river reach features (e.g. gravel bars, meander bends, riffle pool sequences) also create zones of upwelling and downwelling flow (Tonina and Buffington 2007; Figure 1.7). Together, these flow dynamics create complex hydrologic, biogeochemical and ecological patterns in alluvial rivers (Fisher *et al.* 2004, Arscott *et al.* 2005, Stanford *et al.* 2005).

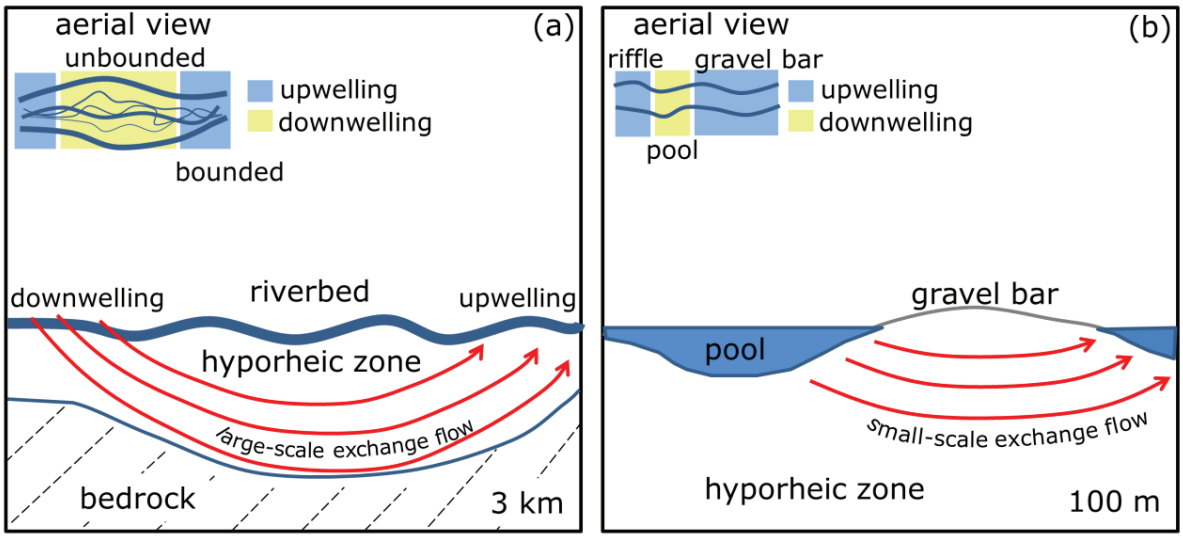

Figure 1.7 Hypothetical diagram of vertical exchange flows between the river surface and hyporheic zone at large-scales over bounded and unbounded river sections (a) and smaller scale river reach features (*e.g.* riffle, pool, gravel bar)(b).

1.5.2 Global distribution of alluvial rivers

Alluvial rivers are distributed globally, spanning large parts of the western North America (Stanford *et al.* 2005), central Asia (Tockner *et al.* 2009) and New Zealand (Gray and Harding 2007). For example, braided alluvial rivers (*i.e.* those that flow in multiple, mobile channels across the floodplain) occur in 163 river systems in New Zealand and have a combined habitat area of 248 400 ha (Gray and Harding 2007). Alluvial rivers are also common in the glaciated mountain regions of Western Europe such as the Alps, Apennines and Pyrenees (Piégay *et al.* 2009). In the Rhône-Mediterranean region of southeast France, there are approximately 650 km of braided alluvial rivers.

1.5.3 Use of alluvial rivers as model systems to study invertebrate community resilience

Alluvial rivers represent ideal systems to study invertebrate community resilience because they i) are naturally harsh systems with frequent surface drying events and ii) provide multiple sources of colonization (Figure 1.8). Disturbances in the form of flooding and drying occur frequently in alluvial rivers, especially along braided reaches (Doering *et al.* 2007, Tockner *et al.* 2009). In southern France, braided reaches experienced as many as 28 over-bank flood events between 1990 and 2000 (Belletti *et al.* 2014). Drying occurs naturally in these systems where there are large-scale zones of downwelling surface water (*e.g.* Doering *et al.* 2007, Capderrey *et al.* 2013). Together, these disturbances place harsh environmental constraints on aquatic invertebrates (Tockner *et al.* 2010) and taxa persisting in alluvial rivers have been shown to be highly resilient to disturbances, mostly flooding (Scrimgeour *et al.* 1988, Matthaei *et al.* 1997, Fowler 2004).

A mosaic of habitats, formed by the continuous restructuring of alluvial river channels (*i.e.* Shifting Habitat Mosaic; Stanford *et al.* 2005), could facilitate high community resilience by providing multiple sources of colonization (Arscott *et al.* 2005, Figure 1.8). Frequent flooding along braided reaches can reshape up to 60% of aquatic habitat in less than 2.5 years due to the high mobility of unconsolidated substrate (Van Der Nat *et al.* 2003, Datry *et al.* 2014). This process increases channel heterogeneity by forming bars, islands, oxbows, backwaters and new channels that are differentially exposed to flooding and drying (Ward *et al.* 2002). Additionally, the large-scale upwelling zones in alluvial rivers may provide perennial flowing habitats (Malard *et al.* 2002, Capderrey *et al.* 2013). Together, the relative proportion of these habitats changes little over time despite spatial turnover (*i.e.* shifting mosaic steady-state; Arscott *et al.* 2002) and therefore provide sources of colonization longitudinally (*e.g.* upstream), laterally (*e.g.* backwaters) and vertically (*e.g.* hyporheic zone) across the riverscape.

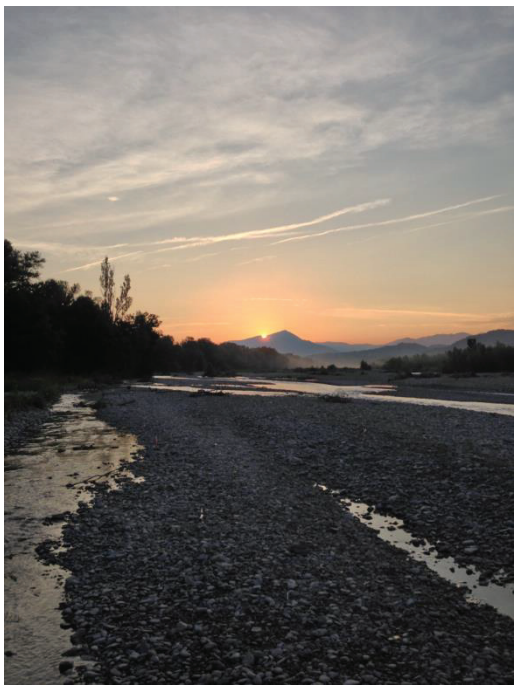

Figure 1.8 Photograph of the alluvial Eygues River in southern France. The Eygues River is a braided river with 3–4 channels across a broad floodplain, an expansive hyporheic zone due to coarse, unconsolidated substrate helps form a mosaic of potential sources of colonization.

1.6 Research objective and questions

As introduced previously, disturbances play a fundemental role in community ecology because they influence the processes that determine community assembly. Aquatic ecosystems are becoming increasingly disturbed due to global climate change and other anthropogenic pressures such as water abstraction. However, our understanding of how aquatic communities respond to disturbances, such as drying, has rarely considered those in naturally harsh ecosystems, which could be less affected by

drying because of a strong environmental filtering effect that could promote high resilience. Furthermore, there remains a lack of empirical evidence that quantifies the potential sources of colonization, such as the hyporheic zone, that drive community resilience. Therefore, these knowledge gaps inhibit our ability to predict the effects of drying on communities and focus management efforts that will increase community and ecosystem resilience to future global changes. In this thesis, my objective was to explore aquatic invertebrate community resilience in alluvial rivers, a naturally highly disturbed ecosystem, by quantifying their resilience to drying and identifying the primary source of colonists contributing to this resilience. To this end, I used 4 congrous field and laboratory mesocosm experiments:

In the first study (Figure 1.9, Chapter 3), I addressed community resilience to drying (moderate or severe) across 8 alluvial rivers by assessing community richness, abundance, composition and functional diversity in intermittent and perennial reaches within the same river both before and after drying. I predicted that moderate drying (< 1 mo. duration) would not affect communities because they would be comprised of taxa with strategies that promote their resistance and resilience. Furthermore, I tested if severe drying (> 3-fold increase in maximum drying duration) would affect communities. I predicted that there would be differences between communities experiencing severe drying events and communities in perennial reaches because strategies of resistance and resilience should be less effective as drying duration increases and the availability of refuges decreases.

In the second study (Figure 1.9, Chapter 4), I identified the primary source of colonists that drives high community resilience in an alluvial river by drying channels and assessing community resilience in channels where drifting invertebrates were either allowed or blocked following flow resumption. I predicted that blocking drift would alter invertebrate taxonomic and functional richness, density and evenness and alter composition because drift is expected to be the primary source of colonists. I also predicted that blocking drift may lower mean invertebrate body size because colonizers from other sources (*e.g.* hyporheic zone, aerial, resistance forms) are expected to be smaller than those arriving via drift.

Based on the results from this study, which indicated high community resilience was attributable to colonization from the hyporheic zone, I aimed to further examine invertebrate use of the hyporheic zone.

In the third study (Figure 1.9, Chapter 5), I used laboratory mesocosms to examine the effects of increasing water temperature and intra-specific competition, two environmetnal factors that generally increase before surface water disappears, on the vertical migration of *Gammarus pulex* (Crustacea: Amphipoda) into the hyporheic zone. I predicted that *G. pulex* would avoid both increasing water temperature and competition by migrating into the hyporheic zone. Additionally, I predicted use of the

hyporheic zone, which is food-limited, would have negative effects on the survival, leaf mass consumption and energy stores of *G. pulex*.

In the fourth study (Figure 1.9, Chapter 6), I tested how use of the hyporheic zone as a refuge during drying by two populations of *G. pulex,* from intermittent and perennial rivers, is affected by changes in the water table depth in mesocosms. I predicted that increasing the water table depth would reduce survival and the proportion of *G. pulex* that returned to the surface because organisms would be more likely to become stranded in dry substrate and thus face higher risk of desiccation. I also predicted that this would have cascading effects of leaf litter decomposition and energy stores of invertebrates as a result of fewer organisms returning to the surface to feed on leaf litter and higher energetic costs of migrating further into the hyporheic zone. Additionally, I evaluated differences in the hyporheic zone use between the two populations which may indicate local adaptation to drying through use of the hyporheic zone.

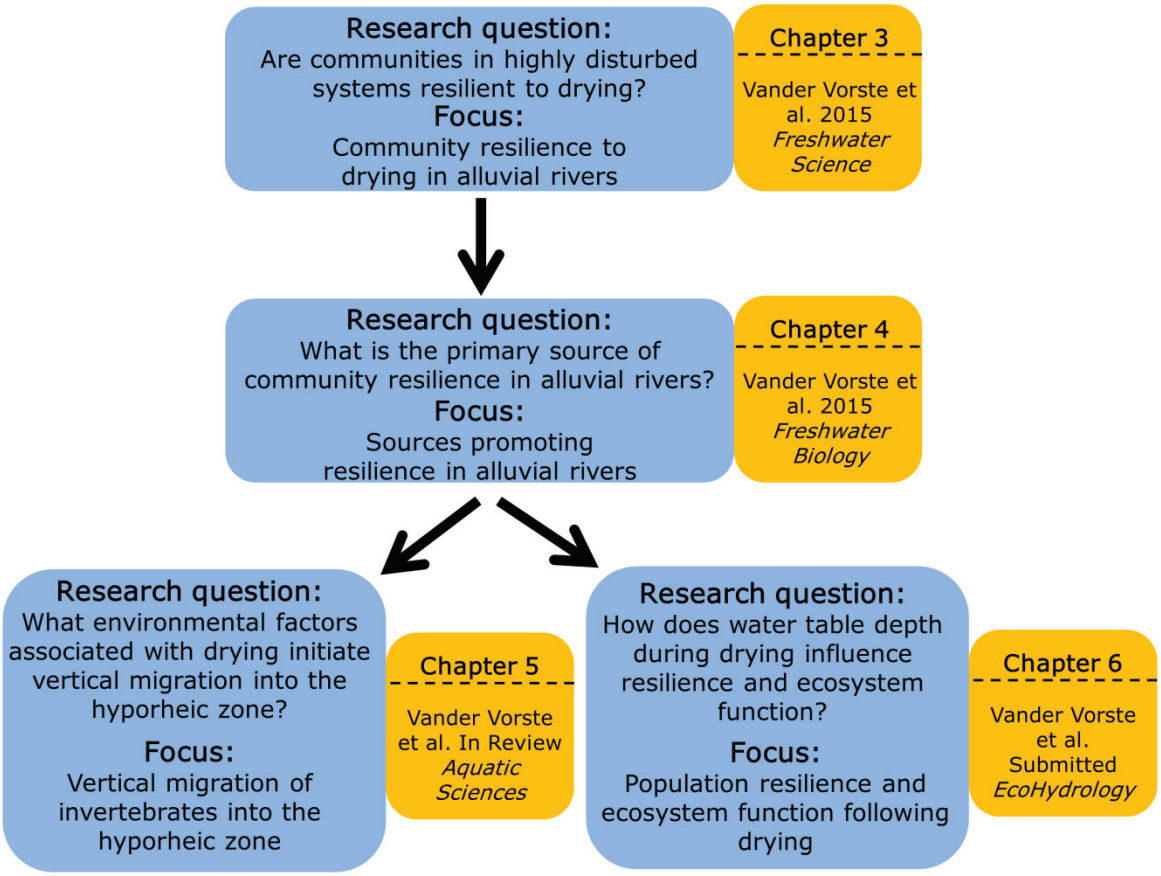

Figure 1.9 Research questions and focus of the 4 studies presented in chapters 3-6 of this thesis.

CHAPTER 2:

MATERIALS & METHODS

Chapter 2: Materials and Methods

In this thesis, I used a combination of field observations (Chapter 3), manipulative field experiments (Chapter 4) and laboratory mesocosm studies (Chapter 5, 6) to address my research objectives. Below, I will discuss two novel experimental approaches developed in this thesis. Further details of the materials and methods used are given within their respective chapters.

2.1 Reach-scale manipulative field experiments

To quantify the potential importance of drift as a source of colonization following drying, I designed a study to dry channels and then manipulate drift during a 4 week period re-wetting period. I chose to work at the reach-scale because it is the most relevant scale for studying the effects of disturbances such as flooding and drying on communities (Englund and Cooper 2003). Reach-scale manipulations are relatively rare in aquatic ecosystems, especially when studying the relative contributions of different sources of colonization (Townsend and Hildrew 1976, Williams and Hynes 1976, Fowler 2002, Bruno *et al.* 2012). During this experiment, a team (i) placed diversion dams to redirect water away from the study channel and create a drying event lasting one-week (Figure 2.1a) and then (ii) re-directed water into the channels to allow for colonization either with (n = 3 channels) or without drift (n = 3 channels; Figure 2.1b). Processes of colonization (vertical migration, aerial oviposition, and desiccation-resistance) were measured during the study period to quantify their potential to promote resilience (Figure 2.1c-f).

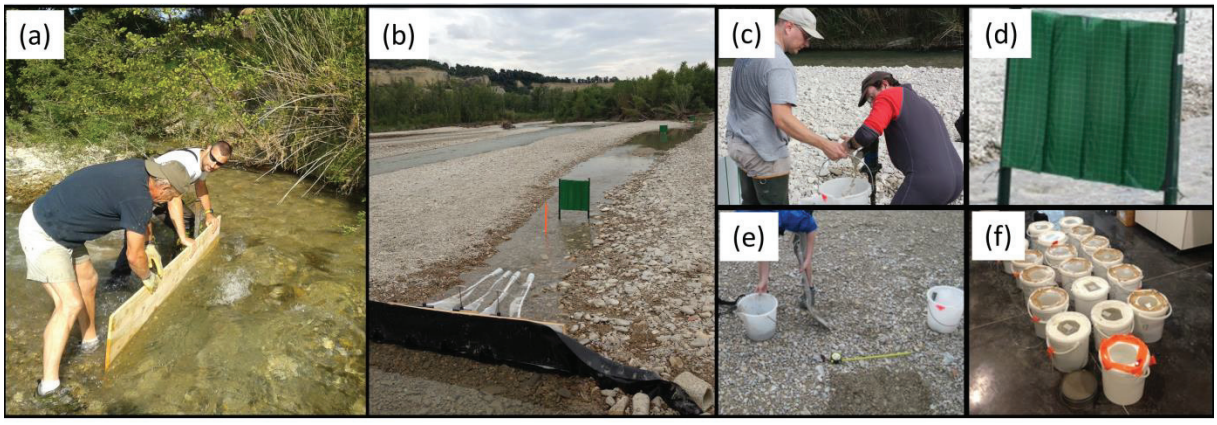

Figure 2.1 Photographs showing placement of diversion dams to dry channels (a), re-direction of water into the channels to allow colonization (b) and collection of invertebrates that colonize by vertical migration from the hyporheic zone (c), aerial oviposition (e) and desiccation-resistance (e, f).

2.2 Laboratory mesocosm design and application

To further examine specific environmental factors that could influence invertebrate response to drying and use of the hyporheic zone in alluvial rivers, I designed and constructed laboratory mesocosms

which simulated conditions of the surface and hyporheic zones in an alluvial river (Figure 2.2a). I chose laboratory mesocosms because they allowed me to manipulate environmental factors that I hypothesized to be important in the use of the hyporheic zone by invertebrates, while controlling other factors (*e.g.* substrate size, dissolved oxygen) that could potentially influence vertical migration. In my first experiment using mesocosms (Chapter 5), I manipulated water temperature and intra-specific competition to examine their effects on vertical migration of *G. pulex* into the hyporheic zone. Water temperature in the hyporheic zone was controlled by the temperature of inflowing water (15°C) and in the surface zone through the use of aquarium heating cables, allowing a maximum temperature difference between the two zones of 10°C (15–25°C). Intra-specific competition was induced by increasing the number of organisms placed in each mesocosm, while keeping the amount of leaf litter constant. In the second mesocosm experiment (Chapter 6), I simulated a one-week drying event and manipulated the depth of the water level (below the surface) to test its effect on the use of the hyphorheic zone as a refuge by *G. pulex* (Figure 2.2b). Following each of these experiments, invertebrates were collected from the hyporheic and surface zones, respectively, by separating the mesocosms into two sections before substrate was sieved (Figure 2.2c). I created a video to help visualize mesocosm design, construction and application available at http://dx.doi.org/10.6084/m9.figshare.1544573.

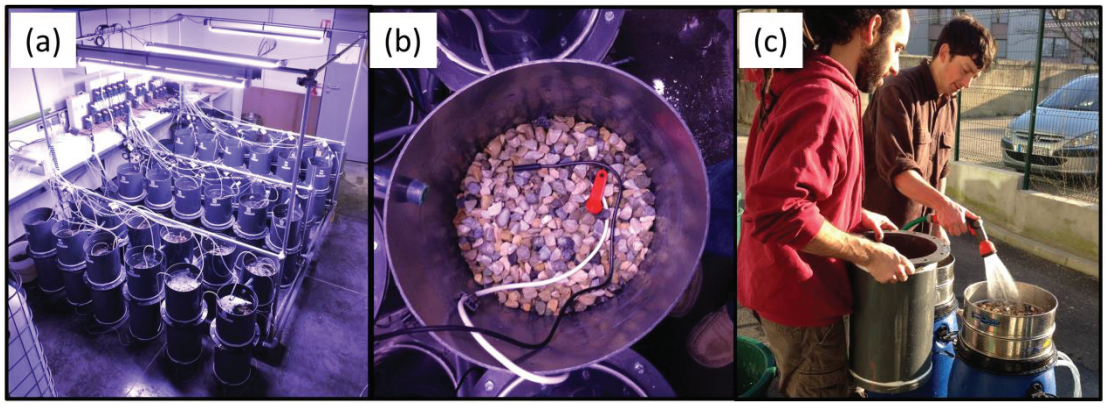

Figure 2.2 Photographs of laboratory mesocosms (a) used to test the effects of water temperature and intra-specific competition (Chapter 5) and depth of the water table during drying events (Chapter 6)(b). At the end of each experiment, mesocosms were separated into two sections to collect invertebrates from hyporheic zones and surface zones separately (c).

CHAPTER 3:

INVERTEBRATE COMMUNITIES IN GRAVEL-BED, BRAIDED RIVERS ARE HIGHLY RESILIENT TO FLOW INTERMITTENCE

A version of this chapter has been published: Vander Vorste R, Corti R, Sagouis A, and T. Datry (2015). Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence. Freshwater Science: doi:10.1086/683274.

Chapter 3: Invertebrate communities in gravel-bed, braided rivers are highly resilient to flow intermittence.

3.1 Abstract

In naturally disturbed systems, harsh environmental conditions act as filters on the regional species pool, restricting the number of taxa able to form a local community to those having adaptive resistance and resilience traits. Thus, communities in highly disturbed ecosystems may be less sensitive to a given disturbance than those in less disturbed ecosystems. We explored this idea by examining the response of aquatic invertebrate communities to flow intermittence in gravel-bed, braided rivers (BRs). Flow intermittence is considered a major driver of communities in rivers, but its influence on communities in BRs, which are recognized as naturally, highly disturbed environments, is relatively unexplored. We used a multisite Before-After–Control-Impact design to quantify the effects of drying events of different durations (moderate: 2–3 wk, severe: 1–3 mo) on invertebrate communities in 8 BRs in southeastern France. As predicted, no effects of flow intermittence were detected 1 to 4 mo after flow resumption on taxonomic richness, composition, or functional diversity of communities facing moderate drying events. Communities subjected to severe drying events were similar to those in perennial reaches as few as 19 d after flow resumption. Moreover, communities showed functional redundancy and no loss of functional diversity after drying events. These results differ from those of studies in other river systems, where persistent effects of flow intermittence on communities generally have been found, and highlight the need for cross-system comparisons that explore the effects of drying on communities. Identifying the processes (e.g., niche-selection, cotolerance) and habitat features (e.g., hyporheic zone refugia) that promote community resilience in BRs will advance our understanding of how anthropogenic stressors and climate change may affect communities in freshwater ecosystems.

Key words: resistance, resilience, recovery, co-tolerance, hyporheic zone, alluvial rivers, BACI design

3.2 Introduction

One pervasive goal of community ecology is to identify processes that determine variation in taxonomic richness, composition, and abundance of communities (Leibold et al. 2004, Vellend 2010). Disentangling the different processes involved in community assembly and the spatiotemporal scales at which they operate and interact is essential to predict the responses of communities to future environmental changes (Götzenberger et al. 2012). At broad scales, evolutionary processes, climate (e.g., precipitation and temperature regime), and historical events act together to determine a regional

species pool (Poff et al. 1997). Furthermore, the potential for taxa in the regional species pool to form a local community is a function of a series of selective filters, including the abiotic environment and biotic interactions, which operate over multiple nested habitat levels (Leibold et al. 2004). Thus, the persistence of a taxon in a local community depends on whether it possesses a combination of traits (life-history, morphological, mobility and ecological) to pass through multiple habitat filters (niche theory; Whittaker et al. 1973).

In naturally disturbed ecosystems, abiotic environmental conditions border on extreme values and are often unstable or stochastic, so fewer taxa from the regional species pool are available to form a local community (Chase 2007, Lepori and Malmqvist 2009). Therefore, taxa rely on combinations of traits (i.e., strategies sensu Southwood 1988) that promote resistance, resilience, or both to disturbances (Stanley et al. 1994, Fritz and Dodds 2004). Resistance is the capacity of a taxon, a community, or ecosystem to persist unchanged through a disturbance, whereas resilience is its capacity to recover (return to predisturbance levels, or similarity with undisturbed sites) after the disturbance (Stanley et al. 1994, Datry et al. 2014a). Resistance strategies generally include physiological and morphological traits (e.g., resistance to heat or to shear stress), whereas resilience strategies are related to movement/dispersal from sources of colonization (Williams 2006). Furthermore, traits that enhance resistance and resilience to one type of disturbance also can increase tolerance to other disturbances, a concept termed positive cotolerance (Vinebrooke et al. 2004). Consequently, communities in very disturbed ecosystems, where multiple and disparate disturbances occur with relatively high frequency, may show a limited response to a discrete disturbance (Vinebrooke et al. 2004, Côté and Darling 2010).

Gravel-bed, braided rivers (BRs) provide an archetype of naturally, highly disturbed ecosystems, making them good systems in which to explore the response of communities to disturbances (Tockner et al. 2010). In BRs, multiple disturbances occur frequently in the form of predictable and stochastic floods and drying events (Arscott et al. 2002, Tockner et al. 2010). Habitat turnover rates are extremely high in BRs. For instance, 60% of the aquatic habitat can change to terrestrial habitat in <2.5 y because of bed-scouring and channel movements (van der Nat et al. 2003). During periods of low flow, most, if not all, of the braided channel network becomes dry in areas of large-scale downwelling where surface water infiltrates into the ground water. In contrast, areas of large-scale upwelling generally have perennial surface flow (Malard et al. 2003, Doering et al. 2007). Despite the physically harsh environmental conditions, BRs harbor, at the catchment-scale, rich invertebrate communities composed of taxa with resistance and resilience strategies (e.g., Arscott et al. 2002, Gray and Harding 2007).

BRs experience multiple natural disturbances, but most research has focused on the effects of floods (e.g., Scrimgeour et al. 1988, Olsen and Townsend 2005), leaving the response of communities to

channel drying relatively unexplored (but see Sagar 1983, Fowler 2004). Flow intermittence (i.e., the periodic loss of surface water in river channels) is considered a major driver of river communities and can induce declines in taxonomic richness and shifts in community composition and functional diversity that may persist for several months to years after flow resumption (e.g., Arscott et al. 2010, Bogan et al. 2013, Datry et al. 2014a). However, communities in BRs may be less affected by drying than those from other intermittent rivers because their constituent taxa possess traits that promote resistance and resilience. For example, invertebrate taxa in habitats subject to frequent floods and bed-scouring possess traits, such as small body size and high mobility, that allow them to navigate interstitial spaces in river beds to escape harsh surface flows (Townsend and Hildrew 1994, Statzner and Bêche 2010). These same traits allow taxa in intermittent reaches to recover quickly after drying by migrating from nearby drying refuges (Bonada et al. 2006, Robson et al. 2011), including the underlying hyporheic zone (i.e., saturated interstitial areas beneath the riverbed; White 1993), which is expansive in BRs (Capderrey et al. 2013). However, the factors that promote the resistance and resilience of communities may be curtailed by the duration or severity of drying events, which is considered as one of the main flow-regime components driving the response of communities (e.g., Poff et al. 1997, Lytle and Poff 2004). Severe drying events often are associated with greater distance to sources of colonization (e.g., Larned et al. 2011) and dry hyporheic sediments (e.g., Boulton 2003, Datry 2012). Therefore, the effects of channel drying on communities may differ depending on the duration of drying events (Lake 2003, Datry et al. 2014a).

We addressed the effects of flow intermittence on taxonomic richness, composition, and functional diversity of aquatic invertebrate communities across 8 BRs in southeastern France. We used a multisite Before-After–Control-Impact design to quantify the effects of drying events of different durations (moderate: 2–3 wk, severe: 1–3 mo) on these communities. We predicted that moderate drying events would have no detectable effects on communities because taxa are frequently exposed to multiple disturbances and, therefore, have strategies that promote their resistance and resilience. Moreover, we predicted that severe drying events would alter communities because resistance and resilience strategies of taxa will be less effective as channel drying becomes exacerbated and the availability of refugia, including saturated hyporheic sediments, decreases with increased drying duration.

3.3 Methods

3.3.1 Braided rivers and study reaches

We studied 8 BRs in southeastern France, a region that contains a high concentration of BRs in the Alps (Piégay et al. 2009; Figure 3.1, Table 3.1). These rivers are influenced or dominated by a

Mediterranean climate, including mild, rainy springs and hot, dry summers (Piégay et al. 2009). Flow regimes in Mediterranean rivers are characterized by floods and drying events that are more stochastic, frequent, and intense than those in rivers in temperate climate zones (Bonada et al. 2007). For example, in addition to frequent summer drying events, BRs in this region had up to 28 over-bank flood events between 1990 and 2000 (Belletti et al. 2014).

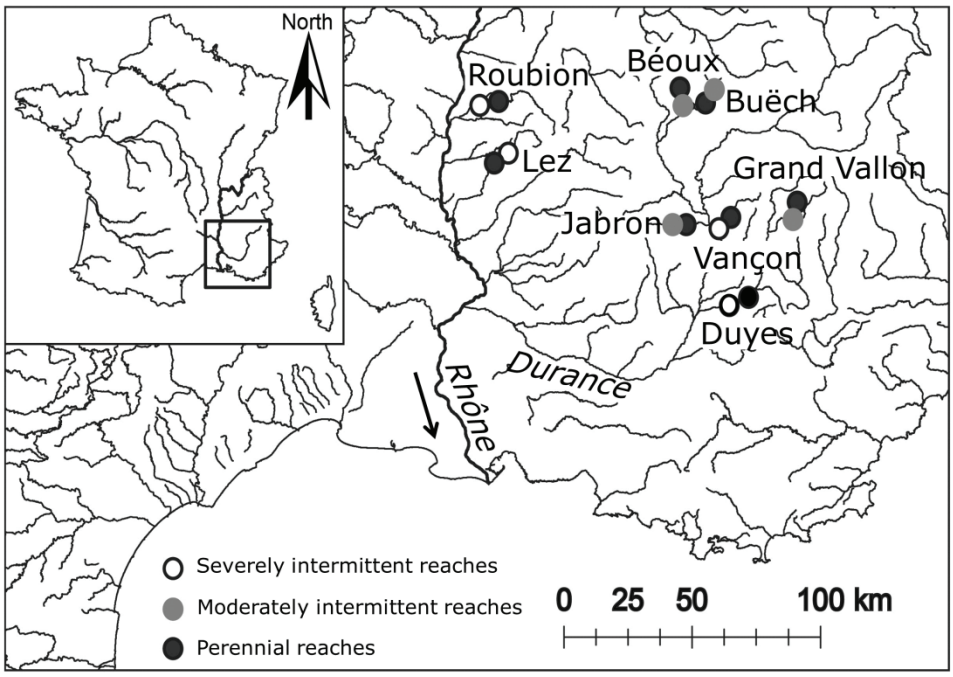

Figure 3.1 Location of the intermittent and perennial reaches across 8 gravel-bed, braided rivers in southeastern France.

Table 3.1 Mean annual discharge (m^3/s), river length (km), distance between reaches (km), active channel width (m), and reach width (m) across 8 braided rivers that experienced moderate or severe drying events.

Drying class	River	Reach type	Catchment area (km^2)	Annual discharge (m^3/s)	River length (km)	Distance between reaches (km)	Elevation (m)	Active channel width (m)	Reach width (m)
Moderate	Béoux	Intermittent	389	–	17.3	2.2	874	141	4–5
		Perennial					923	31	4–5
	Buëch	Intermittent	389	2.1	44.5	2.8	895	98	3–5
		Perennial					869	70	3–5
	Grand Vallon	Intermittent	332	–	19.2	0.7	638	42	1–2
		Perennial					626	58	1–2
	Jabron	Intermittent	205	3.2	36.5	5.8	482	278	5–6
		Perennial					462	61	5–6
Severe	Duyes	Intermittent	124	1.9	25.2	1.8	396	37	2–5
		Perennial					515	47	2–5
	Lez	Intermittent	445	1.3	73.5	4.0	208	77	3–4
		Perennial					178	77	2–3
	Roubion	Intermittent	612	1.9	66.0	1.2	190	30	2–5
		Perennial					187	12	2–5
	Vançon	Intermittent	112	–	30.2	0.3	466	140	2–5
		Perennial					468	51	3–5

The focal BRs are 17 to 74 km (mean ± SD, 39 ± 21 km) in length, with catchment areas from 112 and 612 km^2 (326 ± 171 km^2) and have mean annual discharge from 1.3 to 3.2 m^3/s (2.1 ± 0.7 m^3/s; Table 3.1). For each river, we selected an intermittent reach that underwent drying during the study period (May–November 2011) and a nearby perennial reach that flowed throughout the study period (Figure 3.1, Table 3.1). We selected reaches using observations from previous studies (Capderrey et al. 2013), aerial photographs (www.geoportail.fr), and preliminary field visits. Intermittent reaches were in downwelling areas, typically characterized by a wide and active braided band and a large valley bottom (Capderrey et al. 2013). At these reaches, surface water was completely absent during drying events and disconnected pools persisted only for ≤1–2 d because of high hydraulic conductivity of the river bed. Perennial reaches were upstream (n = 3) or downstream (n = 5) of the intermittent reaches (mean distance = 2.4 ± 1.8 km; Table 3.1) in areas with narrow active braided channel and valley bottoms (Figure 3.1). In all rivers, segments with perennial flow were present upstream of intermittent study reaches. The braided active channel was 12–278 m wide (78 ± 65 m), whereas the mean wetted width of study reaches, measured before and after drying, was 1–6 m (Table 3.1).

3.3.2 Quantification of flow intermittence

At each reach, we continuously monitored the presence or absence of surface water from 4 May to 1 December 2011 using Onset Hobo® water state loggers (Intermountain Environmental, Inc., Logan, Utah). The loggers consisted of a water-state data logger, submersible case, coated cable (length = 10 m), and water presence sensor. A detailed description of the loggers and their installation are provided in Appendix 3.1.

3.3.3 Invertebrate community sampling

We collected benthic invertebrates from each reach in 2 sampling periods, spring (4–12 May 2011) and autumn (21–30 November 2011), which occurred before (≥5 d) and after (≥19 d) summer drying events, respectively. At each reach, we selected 3 runs to minimize between-habitat variability among reaches, including the 1–3 runs at which loggers had been installed. Within each run, we randomly collected 2 benthic invertebrate samples with a Hess sampler (diameter = 40 cm, area = 0.125 m^2, 200-µm mesh) for a total of 192 samples (6 samples/reach × 2 reaches/river × 8 rivers × 2 sampling periods). We preserved samples with 96% ethanol and counted and identified all invertebrates to the lowest practical taxonomic level in the laboratory. We identified all mollusks and most insects to the level of genus, and crustaceans, annelids, and mites to the level of genus, family, or order.

3.3.4 Data analysis

3.3.4.1 Quantification of flow intermittence across reaches

For each run where loggers were installed, we quantified flow intermittence based on total number (*n*, events), total duration (D_{total}), mean duration (D_{mean}), and maximum duration (D_{max}) of drying events during the period of record. We also calculated the length of time before the first drying event (T_{before}) and the length of time after the last drying event (T_{after}), relative to the date that invertebrate samples were collected in spring and autumn, respectively. These data confirmed our initial assignment of reaches into intermittent and perennial reach types. We then assigned intermittent reaches into 2 drying classes: moderate drying (n = 4 reaches) when D_{max} was <1 mo and severe drying (n = 4 reaches) when D_{max} was >1 mo. We chose D_{max} to categorize drying severity because it represents the longest continuous drying event experienced by aquatic invertebrate communities during the study period, which sometimes included multiple brief periods (1–2 d) of flow resumption. These 2 drying classes represent drying events in the focal study and do not necessarily match the severity of drying in other types of intermittent rivers (i.e., desert, karstic, polar), where drying events can be longer.

3.3.4.2 Effects of flow intermittence on taxonomic richness and composition of invertebrate communities

We described invertebrate communities at each reach and for each period in terms of taxonomic richness, density (individuals (ind)/m^2), and the proportions (% relative abundance) of EPT (Ephemeroptera, Plecoptera, Trichoptera) and OCHD (Odonata, Coleoptera, Heteroptera, Diptera). The latter 2 metrics commonly change in response to drying events because a shift occurs from lotic (mostly preferred by EPT) to lentic (mostly preferred by OCHD) habitat types that usually precedes complete channel drying (e.g., Williams 2006, Bonada et al. 2006). These metrics were used as dependent variables in linear mixed-effects models with Gaussian error distribution. Density was $\log_{10}(x + 1)$-transformed, and proportion data were $\arcsin\sqrt{(x)}$-transformed to meet the assumptions of parametric analysis. For each dependent variable, models included 2 sampling periods (before, after drying events), 2 reach types (intermittent, perennial), and the interaction term (reach type × sampling period) as categorical fixed factors and river as a random factor (Bolker et al. 2009). We used the significance of the interaction term ($p < 0.05$) to identify a significant effect of drying. We analyzed invertebrate data from moderate ($n = 4$) and severe ($n = 4$) reaches separately. We constructed all linear mixed-effects models using R software (version 2.8.1; R Project for Statistical Computing, Vienna, Austria) *nlme* package (Pinheiro et al. 2014). We calculated effect size and 95% confidence intervals for each richness and composition metric across reach types, regardless of sampling period, for both drying classes (Appendix S2).

We used Adonis, a permutational multivariate analysis of variances (Anderson 2001), to test for the effects of reach type, sampling period, and their interaction on multivariate taxonomic composition. Adonis returns a R^2 statistic that is a measure of separation among groups (0 indicates complete mixing and 1 represents full separation) according to Bray–Curtis dissimilarity values calculated using $\log_{10}(x + 1)$-transformed invertebrate abundance and a p-value estimated by repeated permutations ($n = 999$) of the data. The design included 2 sampling periods (before, after) and 2 reach types (intermittent, perennial), and used river as random factor. We performed Adonis separately for both drying classes.

We used nonmetric multidimensional scaling (NMDS) to visualize compositional changes in invertebrate communities among reach types and sampling periods. First, we calculated dissimilarity matrices using the Bray–Curtis dissimilarity index from the mean $\log_{10}(x + 1)$-transformed invertebrate abundance by sampling period and reach type. Second, we used Procrustes to display spatial ordinations (between-reach) across before and after sampling periods. Procrustes uses uniform scaling (expansion or contraction) and rotation to minimize the squared differences between 2 ordinations (Peres-Neto and Jackson 2001). Within each drying class, the ordinations of all reaches according to their taxonomic composition are shown simultaneously and for each reach, arrows join their respective positions between sampling periods. We performed NMDS, Procrustes, and Adonis statistical procedures with functions in the R package *vegan* (Oksanen et al. 2013).

3.3.4.3 Effects of flow intermittence on functional diversity, trait richness, and composition of invertebrate communities

We compared Rao's quadratic entropy (i.e., functional diversity), trait richness, and composition between sampling periods and reach types. Rao's quadratic entropy is an abundance-weighted metric that measures the mean pairwise dissimilarities of randomly selected taxa in a community as a way of describing the breadth of traits present within a community (Rao 1982). Trait richness is measured as the total number of traits represented within the community. Generally, these 2 metrics serve as a proxy of the different ecological roles (i.e., functions) that taxa play in an ecosystem and respond to changes in trait composition (Heino 2005). For these metrics, we characterized invertebrate communities based on 61 traits representing 8 grouping features including: aquatic stage, reproduction, dispersal, resistance form, food, feeding style, respiration and locomotion and substratum relation (Appendix S3; Tachet et al. 2002, Schmera et al. 2015). Trait information was unavailable for 28 of the 105 unique taxa identified, including mostly Diptera, Mollusca, Coleoptera, and Heteroptera. Therefore, we excluded these taxa from analysis of functional diversity, trait richness, and composition analysis. We used a trait database that is fuzzy coded (scores 0–5) according to the affinity of each genus to a particular trait (Tachet et al. 2002). We weighted each trait by multiplying the relative trait affinity scores by the $\log_{10}(x + 1)$-transformed abundance of each taxon with the trait and dividing this value by the total abundance for each sample resulting in a trait × sample matrix (Dray and Dufour 2007). We used this matrix to calculate functional diversity and trait richness in the R packages *ade4* and *vegan*, respectively (Dray and Dufour 2007, Oksanen et al. 2013). We further tested for changes in trait composition with the trait × sample matrix using Adonis as described previously.

We also selected a priori a group of traits, identified as indicators of flow intermittence and active use of the hyporheic zone as a refuge, to test the effects of drying on trait composition (Bonada et al. 2007, Robertson and Wood 2010). These traits included: resistance forms (i.e., eggs, statoblasts, cocoons, diapause, and desiccation resistant cells), small body size (≤9 mm), active aerial dispersion, swimmer habit, burrower or interstitial habit, aerial respiration, and asexual reproduction. We calculated the proportion of taxa in each sample that had the a priori traits using the R package *ade4* (Dray and Dufour 2007). We then tested for the effects of drying on each $\arcsin\sqrt{(x)}$-transformed trait proportion using linear mixed-effects models, as described above, where the proportional values for each trait were used as dependent variables and moderate and severe drying classes were analyzed in separate models. We calculated effect sizes and 95% confidence intervals of functional diversity, trait richness, and composition metrics as described above for the taxonomic metrics (Appendix S2).

3.4 Results

3.4.1 Quantification of flow intermittence across reaches

The moderate reaches underwent 11 ± 8 (mean ± SD) drying events, lasting a total of 43 ± 55 d (D_{total}), with D_{mean} = 5 ± 3 d and D_{max} = 17 ± 4 d (Table 3.2). The severe reaches underwent 8 ± 5 drying events, lasting a total of 104 ± 45 d (D_{total}), with D_{mean} = 24 ± 19 d and D_{max} = 57 ± 35 d. Length of time after the final drying event (T_{after}) was 25 ± 5 d at severe reaches and 81 ± 60 d at moderate reaches (Table 3.2).

Table 3.2 Description of moderate and severe drying events across 8 gravel-bed, braided rivers in terms of total number (*n*, events), total duration (D_{total}, days), mean duration (D_{mean}, days), maximum duration (D_{max}, days) of drying events, length of time before initial drying event (T_{before}, days) and length of time after final drying event (T_{after}, days).

Drying class	River	Reach type	*n* (events)	D_{total} (d)	D_{mean} (d)	D_{max} (d)	T_{before} (d)	T_{after} (d)
Moderate	Béoux	Intermittent	4	18	4.5	16	52	133
		Perennial	No drying events					
	Buëch	Intermittent	15	125	8.3	23	5	28
		Perennial	No drying events					
	Grand Vallon	Intermittent	20	12	1.4	14	70	30
		Perennial	No drying events					
	Jabron	Intermittent	3	15	5.1	14	52	134
		Perennial	No drying events					
Severe	Duyes	Intermittent	7	72	10.2	34	92	30
		Perennial	No drying events					
	Lez	Intermittent	15	59	9.1	30	25	26
		Perennial	No drying events					
	Roubion	Intermittent	5	132	26.5	105	43	26
		Perennial	No drying events					
	Vançon	Intermittent	3	152	50.7	60	25	19
		Perennial	No drying events					

3.4.2 Effect of flow intermittence on taxonomic richness and composition of invertebrate communities

A total of 74,143 invertebrates from 105 taxa was collected from the 8 BRs. Mean density of invertebrates was 2513 ± 3356 ind/m^2 in intermittent and 3635 ± 4921 ind/m^2 in perennial reaches. No reach type × sampling period interactive effect was detected when comparing taxonomic richness, density, or the proportion of EPT and OCHD between moderate and severe reaches (Figure 3.2a–h, Table 3.3). Taxonomic richness and density decreased over the sampling period by 46 ± 24% and 82 ±

12% in perennial reaches, 64 ± 20% and 96 ± 5% in moderate reaches, and 49 ± 27% and 72 ± 15% in severe reaches, respectively (Figure 3.2a–d, Table 3.3). Proportions of EPT and OCHD did not differ among reach types or sampling periods (Figure 3.2e–h, Table 3.3).

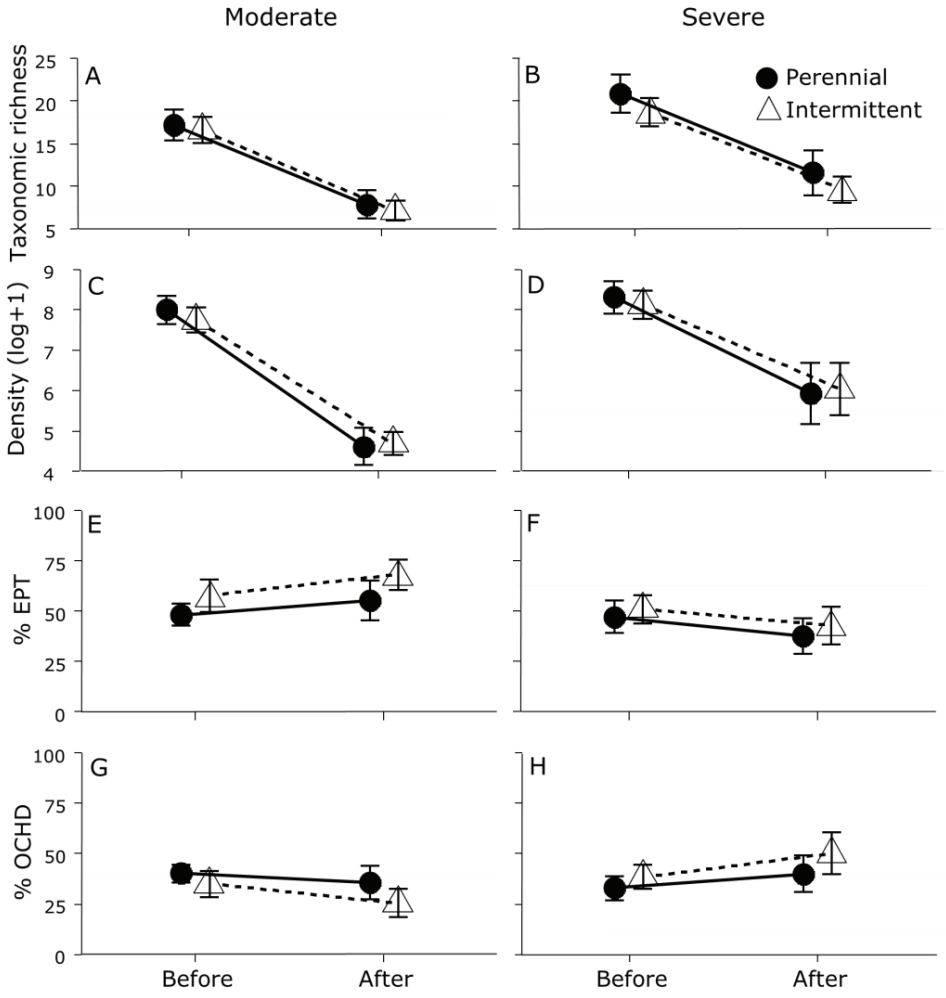

Figure 3.2 Interaction plots showing change from before to after drying of mean (±1 SE) taxonomic richness (A, B), $\log_{10}(x + 1)$-transformed density (individuals/m^2) (C, D), % EPT (Ephemeroptera, Plecoptera, Trichoptera) (E, F), and % OCHD (Odonata, Coleoptera, Hemiptera, Diptera) (G, H) in reaches with moderate (A, C, E, G) and severe (B, D, F, H) drying.

Community composition showed no effects of drying events among reaches and sampling periods, regardless of duration (Adonis, reach type × sampling period interaction, moderate: $p = 0.772$, severe: $p = 0.936$; Figure 3.3a, b). Temporal variability in taxonomic composition (i.e., before–after differences) was high (Adonis, sampling period, moderate: $p = 0.003$, severe: $p = 0.005$) and consistent across reach types (Figure 3.3a, b).

Table 3.3 Linear mixed-effects models testing the effects of sampling period (before vs after) and reach type (perennial vs intermittent), and their interaction on taxonomic richness, $\log_{10}(x + 1)$-transformed density (individuals/m^2), and the arcsin$\sqrt{(x)}$-transformed % EPT (Ephemeroptera, Plecoptera, Trichoptera) and % OCHD (Odonata, Coleoptera, Hemiptera, Diptera).

Drying class	Variable	Source of variation	df	*F*	*p*
Moderate	Taxonomic richness	Intercept	80	39.95	<0.0001
		Sampling period	6	82.87	<0.0001
		Reach type	3	0.69	0.4683
		Reach × period	6	1.52	0.2643
	Density	Intercept	80	170.69	<0.0001
		Sampling period	6	158.24	<0.0001
		Reach type	3	2.35	0.2226
		Reach × period	6	1.27	0.3020
	% EPT	Intercept	80	56.46	<0.0001
		Sampling period	6	3.89	0.0961
		Reach type	3	5.76	0.0959
		Reach × period	6	1.10	0.3347
	% OCHD	Intercept	80	34.48	<0.0001
		Sampling period	6	4.16	0.0874
		Reach type	3	3.05	0.1790
		Reach × period	6	0.70	0.4352
Severe	Taxonomic richness	Intercept	80	29.3	<0.0001
		Sampling period	6	18.98	0.0048
		Reach type	3	0.94	0.4035
		Reach × period	6	0.01	0.9546
	Density	Intercept	80	64.01	<0.0001
		Sampling period	6	22.54	0.0032
		Reach type	3	0.01	0.9324
		Reach × period	6	0.09	0.7768
	% EPT	Intercept	80	27.34	<0.0001
		Sampling period	6	3.63	0.1054
		Reach type	3	0.83	0.4304
		Reach × period	6	<0.01	0.9841
	% OCHD	Intercept	80	38.48	<0.0001
		Sampling period	6	0.71	0.4332
		Reach type	3	0.36	0.5890
		Reach × period	6	0.04	0.8468

3.4.3 Effects of flow intermittence on functional diversity, trait richness, and composition of invertebrate communities

Flow intermittence did not affect functional diversity, trait richness, or composition (Figure 3.4a–h, Table 3.4). No interactive effect of sampling period × reach type interaction was detected when comparing functional diversity and trait richness between moderate and severe reaches (Figure 3.4a–d,

Table 3.4). Trait composition among reaches was unaffected by drying events, regardless of drying class (Adonis, moderate: reach type × sampling period interaction, $p = 0.663$, severe: $p = 0.795$). Furthermore, no interactive effect of reach type × sampling period was detected on resistance forms (Figure 3.4e, f), small body size (≤9 mm; Figure 3.4g, h; Table 3.4), active aerial dispersion, swimmer habit, burrower or interstitial habit, aerial respiration, or asexual reproduction (data not shown) (linear mixed-effects models, $p > 0.05$).

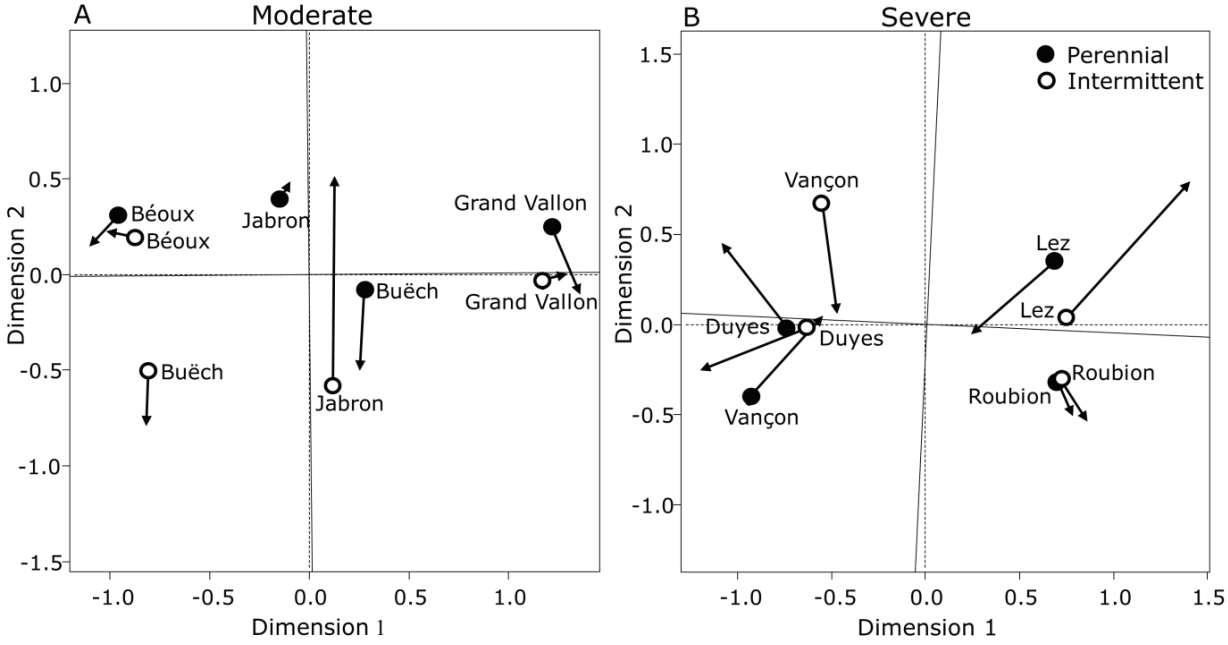

Figure 3.3 Two-dimensional nonmetric multidimensional scaling (NMDS) plots with Procrustes superimposition based on $\log_{10}(x + 1)$-transformed density of invertebrates in reaches with moderate (A) and severe (B) drying. Arrows represent the differences in ordinations between the before (origin of the arrows) and after sampling periods (end of the arrows).

3.5 Discussion

Invertebrate communities in these 8 BRs were highly resilient to flow intermittence, even after severe drying events. Taxonomic richness, composition, and functional diversity of communities in intermittent reaches after either moderate or severe drying events were similar to those of perennial reaches in as few as 19 d of flow resumption. These results differ from those of many previous studies in which aquatic communities showed persistent effects of flow intermittence (e.g., del Rosario and Resh 2000, Bogan et al. 2013, Datry et al. 2014a). We attribute these results to: 1) high resilience of invertebrate communities in BRs, whose constituent taxa have been filtered by deterministic process (i.e., niche-selection) and may have positive cotolerance to multiple disturbances, and 2) the presence of perennial habitat features, including an expansive hyporheic zone, in which taxa can find refuge during drying events.

Table 3.4 Linear mixed-effects models testing the effects of sampling period (before vs after) and reach type (perennial vs intermittent) and their interaction, on the arcsin√(*x*)-transformed proportion of taxa with resistance forms and small body size (≤9 mm), trait richness, and functional diversity.

Drying class	Variable	Source of variation	df	*F*	*p*
Moderate	% Resistance form	Intercept	80	495.68	<0.0001
		Sampling period	6	0.27	0.6192
		Reach type	3	0.40	0.5704
		Reach × period	6	0.04	0.8412
	% Small body size	Intercept	80	300.39	<0.0001
		Sampling period	6	4.45	0.0795
		Reach type	3	0.42	0.5650
		Reach × period	6	0.33	0.5857
	Functional diversity	Intercept	79	27.56	<0.0001
		Sampling period	6	0.37	0.5630
		Reach type	3	0.85	0.4253
		Reach × Period	6	1.76	0.2326
	Trait richness	Intercept	79	298.13	<0.0001
		Sampling period	6	100.25	0.0001
		Reach type	3	0.09	0.7885
		Reach × Period	6	3.60	0.1067
Severe	% Resistance form	Intercept	80	423.50	<0.0001
		Sampling period	6	1.77	0.2315
		Reach type	3	0.11	0.7606
		Reach × Period	6	<0.01	0.9485
	% Small body size	Intercept	80	458.90	<0.0001
		Sampling period	6	0.15	0.7078
		Reach type	3	0.08	0.7942
		Reach × period	6	0.12	0.7408
	Functional diversity	Intercept	79	49.76	<0.0001
		Sampling period	6	0.03	0.8719
		Reach type	3	2.13	0.2406
		Reach × period	6	0.12	0.7367
	Trait richness	Intercept	79	327.17	<0.0001
		Sampling period	6	10.24	0.0186
		Reach type	3	0.51	0.5273
		Reach × period	6	0.12	0.7455

3.5.1 Response of invertebrate communities to flow intermittence in BRs

Flow intermittence is considered a primary driver of community structure and composition in rivers (Arscott et al. 2010, Larned et al. 2010, Datry et al. 2014b). In a broad-scale meta-analysis, Datry et al. (2014a) found that taxonomic richness decreased linearly along gradients of flow intermittence, without considering sampling period, in 14 rivers in Europe, North America, and New Zealand.

Moreover, strong differences in taxonomic richness and density (see Appendix S2 for effect sizes) generally are found between perennial reaches and reaches experiencing 2–15 mo of channel drying (e.g., del Rosario and Resh 2000, Price et al. 2003, Santos and Stevenson 2011, Bogan et al. 2013). Nevertheless, we found no differences in taxonomic richness and density between intermittent and perennial reaches across these 8 BRs. Furthermore, the mean effect sizes (Hedges' *d*) in our study were 8× smaller than those found in previous studies (mean = –0.25 ± 0.3 vs –1.96 ± 1.16), where communities in intermittent reaches had lower taxonomic richness and density than perennial reaches, even after 2 mo of flow resumption (Appendix S2). Our results were consistent after both moderate and severe drying events, despite a >3-fold increase in the maximum duration of drying events (mean D_{max} = 16 vs 57 d). Decreases in taxonomic richness and density that occurred over the sampling period were observed across both intermittent and perennial reaches and, therefore, could not be attributed to flow intermittence. Field observations (see Methods) and examination of continuous flow data for the 3 BRs where flow gauging stations were colocated (Buëch, Lez, Roubion) indicated that no high-flow events (i.e., higher than the mean annual discharge) occurred between rewetting and the after-drying sampling period. Rather, such decreases may illustrate the background of seasonal variability in invertebrate richness and density that is common in BRs (Tockner et al. 2010).

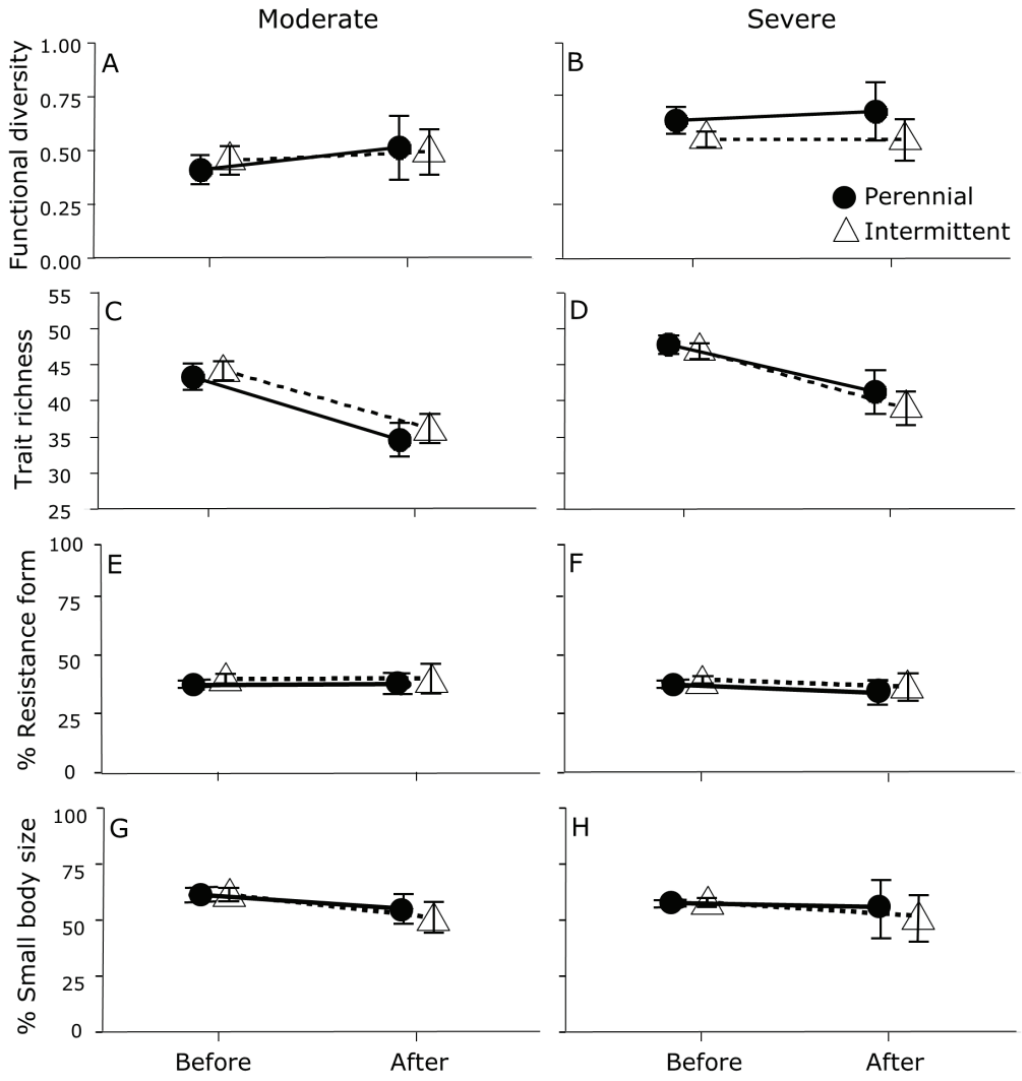

Figure 3.4 Interaction plots showing change from before to after drying of mean (±1 SE) functional diversity (A, B), and trait richness (C, D), proportion of taxa with resistance form (E, F), and small body size (<9 mm) (G, H) in reaches with moderate (A, C, E, G) and severe (B, D, F, H) drying.

Functional diversity and trait composition also can be affected by drying events in freshwater ecosystems (Bonada et al. 2007, Chase 2007). In general, higher proportions of taxa with resistance and resilience traits are found after drying than before and in intermittent vs perennial rivers, indicating that they promote the persistence of invertebrate communities in habitats exposed to drying (Bonada et al. 2006, Datry et al. 2014a). The loss of taxa without these traits after drying may lead to decreases in functional diversity. For example, Chase (2007) found that pond drying reduced the diversity of producers (macrophytes and filamentous green algae) because many of these taxa lacked resistance or resilience strategies. In contrast to these studies, we found no decrease in functional diversity or changes in trait composition following drying events, despite a temporal decrease in taxonomic richness. This result indicates that communities in these BRs have functional redundancy, which occurs when different taxa play similar roles in an ecosystem or possess similar traits, but may

have different sensitivity to disturbances (Rosenfeld 2002). As in arid-land systems (e.g., Boersma et al. 2014), high functional redundancy in BRs may provide insurance against the loss of ecosystem functions when faced with disturbances.

The resilience of invertebrate communities after drying events is comparatively higher in BRs than other intermittent rivers. In our study, recovery occurred in as few as 19 d following severe drying events. Fowler (2004) found that 95% of pre-drying taxa were present after 7 d of rewetting in 2 braided rivers in New Zealand that dried for 6–14 wk. In contrast, Delucchi (1988) reported that 50% of pre-drying taxa remained lost or had reduced abundances after ≥1 mo of rewetting in small–medium forested streams that experienced 1–4-mo drying events. Morrison (1990) reported that recovery of taxonomic richness and abundance took ≥2 mo after 2–3-mo drying events in 4 small streams in Scotland. Most drastically, drying (2–6 mo) had persistent effects on community composition that lasted 1–2 y (Wood and Armitage 2004, Acuña et al. 2005). Other investigators showed that invertebrate communities also may be more resilient to floods in BRs compared to other rivers (Matthaei et al. 1996). Thus, the effects of flow intermittence on invertebrate communities may vary strongly according to river type, and further comparisons may help unravel underlying processes that mitigate these effects of drying.

3.5.2 What might promote community resilience and functional redundancy in BRs?

High resilience and functional redundancy in BRs may be first explained by a strong filtering (i.e., niche-selection) of taxa from the regional species pool with traits allowing them to cope with multiple disturbances (i.e., resistance and resilience; Poff and Ward 1990, Lytle and Poff 2004). When traits enable resistance and resilience of communities to multiple disturbance types, community resilience to a discrete disturbance event is increased (i.e., positive cotolerance; Vinebrooke et al. 2004). For instance, some resilience strategies that allow taxa to disperse to and from refugia during and after floods, including high dispersal ability, inherently promote the recovery of communities after channel drying. Some resistance strategies, such as aerial respiration, allow invertebrates to remain in dry channels until water returns but also help some taxa (e.g., Hemiptera: Belostomatidae) escape flash floods by allowing them to crawl out of the channel to survive in riparian areas (Lytle and Poff 2004). In BRs, the high recurrence rate of disturbances, such as floods and bed-scouring, probably eliminates most taxa that are not also resistant or resilient to drying, thereby reducing the effect of a drying event on the community. However, not all traits that promote resistance and resilience are positively correlated across disturbance types (i.e., negative cotolerance; Vinebrooke et al. 2004). For example, taxa with strong flying ability as adults have inherently larger body size in their aquatic stage. Therefore, their ability to fly long distances to colonize previously dried channels hinders them in the aquatic stage where they are more susceptible to floods than smaller taxa (Townsend and Hildrew 1994). These examples are far from exhaustive but highlight interesting cases of cotolerance in

invertebrate taxa to multiple disturbances. Although not often considered by freshwater ecologists, we think that varying responses of freshwater communities to flow intermittence are partially attributable to positive cotolerance with floods and bed-scouring.

A fundamental habitat feature of BRs that can promote invertebrate community resilience is the complex patterns of surface–groundwater exchanges, occurring at different scales within the often porous, alluvial river bed (Malard et al. 2003, Capderrey et al. 2013). These exchanges add habitat heterogeneity and offer potential drying refuges for invertebrates (Stanford et al. 2005, Capderrey et al. 2013). Perennial reaches, which are a source of drifting and flying invertebrate colonists, are often maintained by large-scale upwelling zones in BRs (Capderrey et al. 2013). In addition, the gravel river beds in most BRs create an expansive hyporheic zone that can be a refuge for benthic invertebrates during periods of flooding and drying (Boulton 2010). However, evidence remains inconclusive for whether benthic taxa seeking refuge in hyporheic zones actually return to the surface after disturbances (but see Holomuzki and Biggs 2007). This uncertainty is a result, in part, of difficulties in quantifying the number of invertebrates that come from the hyporheic zone compared to from other sources (e.g., drift from upstream, aerial oviposition; Dole-Olivier 2011, Stubbington 2012). Recovery of communities after floods and drying occurs as a function of distance to drying refuges, which affects the colonization rate of drifting and flying invertebrates, with faster recovery corresponding to shorter distances (Fritz and Dodds 2004, Robson et al. 2011). Resilience in BRs probably is high compared to other systems because the pattern of surface–groundwater exchanges across alluvial river beds provides potential sources of colonists that are found either directly below the river bed or within several kilometers (<10 km) upstream of previously dry channels.

3.5.3 Conclusions

The current understanding of how communities respond to flow intermittence lags behind other facets of freshwater ecology and merits future research emphasis (Larned et al. 2010, Datry et al. 2014b). Our results suggest that the effects of flow intermittence on invertebrate communities may vary strongly according to river type and call for a cross-system comparison to explore parallels and contrasts and to better understand processes that mitigate the response of communities to drying. As shown in marine systems, such comparisons may reveal that communities in more disturbed systems are also highly resilient because they have a high abundance of disturbance tolerant taxa (Côté and Darling 2010). In addition, the colonization pathways upon rewetting, and notably the question about the importance of the contribution of the hyporheic zone to community resilience deserves more research and, above all, better quantification (Boulton et al. 2010, Dole-Olivier 2011). In the current context of climate change accompanied by increasing flow intermittence and anthropogenic stressors (Larned et al. 2010, Strayer and Dudgeon 2010), understanding and quantifying processes that contribute to ecosystem resilience is essential. Future research in naturally, highly disturbed systems,

such as BRs, could help to advance this understanding and improve the ability to predict the responses of communities to future environmental changes.

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Appendix 3.1 Description and photographs of water state loggers used to quantify flow intermittence.

Water state loggers consisted of an Onset Hobo® (Intermountain Environmental, Inc., Logan, Utah, USA) water state data logger, Onset® submersible case, coated cable (length = 10 m), and water presence sensor (Figure 3.5a). These loggers continuously recorded the timing and frequency of changes in surface water presence and absence. Water, when present, completes the circuit between the 2 exposed copper wires on the sensor and sends a "closed" signal to the logger. During drying, when water no longer completes the circuit, the logger records an "open" signal. In a previous study in the intermittent Albarine River, France (Datry 2012), estimates of drying event duration and frequency provided by these loggers were compared with those from a calibrated hydrological model (ELFMOD; Larned et al. 2011). Datry (2012) found a correlation coefficient of 0.93 between ELFMOD and logger data indicating similar estimates of drying event duration and frequency across 9 sites.

At each reach, we installed loggers in 1–3 runs depending on geomorphic features, in particular the number of braids (channels) present. If ≤ 2 braids were present (13 reaches), we installed 1 logger in a run in the main braid. If > 2 braids were present (3 reaches), we installed loggers in 2 or 3 runs across different braids. In total, we deployed 21 loggers across the 16 study reaches. We attached sensors to a 40-cm metal rod that was hammered into the streambed sediments, so that only the copper wires on the sensor were exposed at the sediment surface (Figure 3.5b). We attached submersible cases containing the data loggers to a nearby tree or metal rod, when trees were not present, and the covered the cables with rocks (Figure 3.5c). In addition, we visually inspected all reaches on 5 occasions during the study period (4 June, 6 July, 16 August, 19 September, 2 November 2011) to ensure loggers were not damaged, validate their records, and check for the occurrence of floods. On the last visual inspection (2 November 2011), we found 4 loggers damaged (*e.g.* sensors removed, cable broken, human tampering). However, the water presence–absence data were retrievable from the loggers, and no additional drying events occurred at these reaches until 1 December 2011, when we removed all loggers from the reaches.

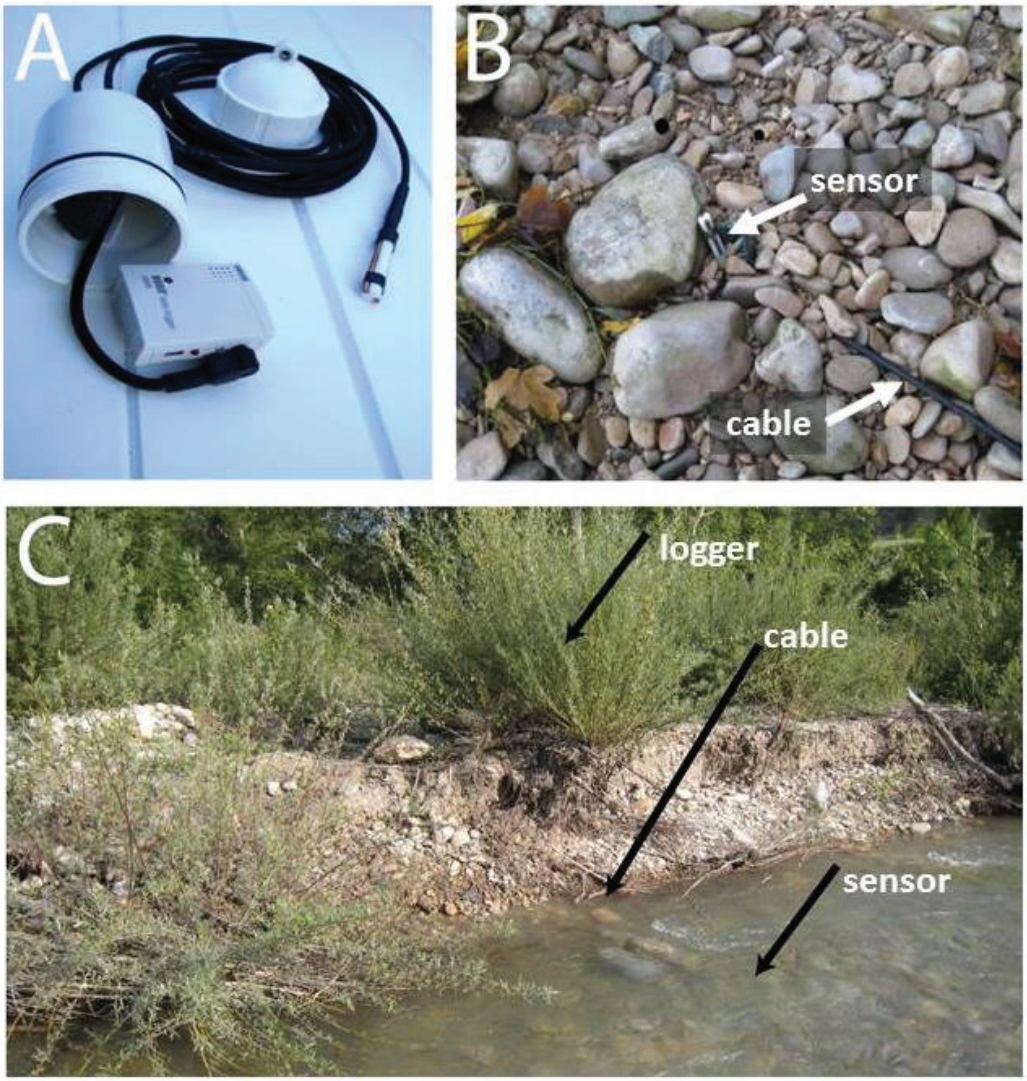

Figure 3.5 Water presence logger and submersible case (a), location of sensor and cable in streambed (b), and placement of the sensor, cable and logger on the streambed and bank (c).

Appendix 3.2 Standardized effect sizes and confidence intervals calculated from this and previous studies that have assessed differences in invertebrate communities between intermittent and perennial streams.

A standard method to calculate standardized effect sizes and confidence intervals based on the results of linear mixed-effects models with random components is still being developed. Therefore, we calculated Hedges' *d* (unbiased effect size) and associated confidence intervals using mean metric values, standard deviations, and sample sizes (Nakagawa and Cuthill 2007). These values represent differences in mean values between intermittent and perennial reaches across before and after sampling periods. These calculations correspond to equations 1, 2, 14, 15, and 17 in Nakagawa and Cuthill (2007). Reporting effect sizes and their confidence intervals improves the interpretation of results and facilitates comparisons among studies by providing estimates of effect magnitude, direction and precision (Nakagawa and Cuthill 2007).

Table 3.5 Effect size (*d* unbiased) including 95% confidence intervals (CI) for metrics used in this study to describe invertebrate community taxonomic richness and composition, functional diversity and trait richness and composition. EPT = Ephemeroptera, Plecoptera, Trichoptera; OCHD = Odonata, Coleoptera, Hemiptera, Diptera.

Drying class		*N*	*d* unbiased	lower 95% CI	upper 95% CI
Moderate	Taxon richness	96	–0.27	–0.67	0.14
	Density	96	–0.20	–0.60	0.20
	% EPT	96	0.53	0.12	0.93
	% OCHD	96	–0.38	–0.78	0.02
	Functional diversity	95	–0.28	–0.68	0.12
	Trait richness	94	–0.07	–0.47	0.33
	% Resistance form	96	0.19	–0.21	0.60
	% Small size	96	–0.11	–0.51	0.29
	% Burrower interstitial	96	–0.27	–0.67	0.13
	% Active aerial	96	0.19	–0.21	0.59
	% Air breather	96	–0.22	–0.22	–0.62
	% Asexual reproduction	no taxa with asexual reproduction present			
	% Swimmer	96	–0.04	–0.44	0.36
Severe	Taxon richness	96	–0.26	–0.66	0.15
	Density	96	–0.25	–0.66	0.15
	% EPT	96	0.17	–0.23	0.57
	% OCHD	96	0.30	–0.10	0.70
	Functional diversity	95	–0.43	–0.84	–0.02
	Trait richness	94	–0.32	–0.73	0.09
	% Resistance form	96	0.17	–0.23	0.57
	% Small size	96	–0.09	–0.49	0.31
	% Burrower interstitial	96	–0.44	–0.84	–0.03
	% Active aerial	96	0.20	–0.20	0.61
	% Air breather	96	–0.47	–0.87	–0.06
	% Asexual reproduction	no taxa with asexual reproduction present			
	% Swimmer	96	–0.16	–0.56	0.24
	Mean		–0.10		
	Minimum		–0.04		
	Maximum		0.53		
	SD		0.22		

Table 3.6 Effect size (*d* unbiased) including 95% confidence intervals (CI), calculated for this study, for metrics used in other studies to describe invertebrate communities of ephemeral (eph.), intermittent (int.) and perennial (per.) streams. * by original study within a null–hypothesis–significance testing–framework (studies include various classes of design).

Metric	Study	Drying duration (mos.)	*N*	*d* unbiased	lower 95% CI	upper 95% CI	Difference detected*
Taxon richness	del Rosario and Resh 2000 per. vs int.	~2	46	–0.84	–1.45	–0.24	yes
	Santos and Stevenson 2011 per. vs eph.	>4	90	–0.73	–1.17	–0.30	yes
	Santos and Stevenson 2011 per. vs int.	<4	108	–0.14	–0.52	0.24	no
	Bogan et al. 2013 per. vs int.	~15	43	–3.57	–4.55	–2.59	yes
	Fenoglio et al. 2007 per. vs int.	~6–8	159	–3.33	–3.81	–2.84	yes
	Miller and Golladay 1996 per. vs int. riffles	~3–4	26	–0.65	–1.45	0.15	yes
	Miller and Golladay 1996 per. vs int. pools	~3–4	30	–0.10	–0.82	0.62	no
	Price et al 2003 per. vs int.	NA	12	1.45	0.15	2.74	no
	Price et al 2003 per. vs eph.	NA	12	–2.40	–3.94	–0.85	yes
Abundance	del Rosario and Resh 2000 per. vs int.	~2	46	–0.70	–1.30	–0.11	yes
	Santos and Stevenson 2011 per. vs eph.	> 4	90	–2.69	–3.27	–2.11	yes
	Santos and Stevenson 2011 per. vs int.	< 4	108	–1.87	–2.32	–1.41	yes
	Fenoglio et al. 2007 per. vs int.	~6–8	150	–2.83	–3.29	–2.37	yes
	Price et al. 2003 per. vs int.	NA	12	–0.42	–1.57	0.73	no
		Mean		–1.34			
		Minimum		–0.10			
		Maximum		–3.57			
		SD		1.45334624			

CHAPTER 4:

IS DRIFT THE PRIMARY PROCESS PROMOTING THE RESILIENCE OF RIVER INVERTEBRATE COMMUNITIES? A MANIPULATIVE FIELD EXPERIMENT IN AN INTERMITTENT ALLUVIAL RIVER.

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Chapter 4: Is drift the primary process promoting the resilience of river invertebrate communities? A manipulative field experiment in an intermittent alluvial river.

4.1 Summary

1. In river systems, aquatic invertebrate communities are surprisingly persistent over time and generally recover quickly from disturbances. Drift has long been viewed as the primary process promoting this resilience and it serves a pervasive role in predictive models of community composition and concepts in lotic ecology. More recently, other processes such as vertical migration from the hyporheic zone, aerial oviposition from distant refuges and the use of resistance forms (e.g. diapause) have received greater recognition and support for their importance.

2. In this study, the view that drift is the primary process promoting invertebrate community resilience was challenged in an intermittent alluvial river using reach-scale flow manipulations. First, six treatment channels were completely dried for one week, while three others were left flowing to be used as controls. Second, flow was re-established in channels and drift was either allowed or blocked for a four-week period. Third, during this period the resilience of community structure, composition and function was compared between treatments and the potential for colonization from the drift, hyporheic zone, aerial oviposition and resistance forms was measured.

3. Communities recovered after only two weeks in all of the previously dried channels and contrary to our hypotheses invertebrate community structure, composition and functional trait composition were not altered by blocking drift, indicating it was not the main process promoting resilience in this river.

4. Three lines of evidence suggested colonization from the hyporheic zone and not aerial oviposition nor resistance forms promoted resilience following rewetting including: (i) finding all common benthic taxa in the hyporheic zone during the drying event, (ii) a distinct decrease in invertebrate size upon rewetting in all treatment channels and (iii) a negative correlation between resilience and water table depth.

5. This experiment highlighted the potential importance of the hyporheic zone as a key source of colonization in alluvial rivers and emphasizes the need for a three-dimensional perspective when considering community resilience in rivers. Adaptive management approaches are needed to direct attention to sources (e.g. hyporheic zone) that are essential to promoting community resilience in rivers facing increased pressures due to climate change, water abstraction and flow regime alteration.

Key words: hyporheic zone, stream drying, braided river, resistance forms, aerial oviposition

4.2 Introduction

Rivers are often viewed as disturbance-prone ecosystems due to their naturally high variations in flow (Resh *et al.*, 1988; Poff *et al.*, 1997). However, river communities are generally persistent over time (e.g. Beche & Resh, 2007) and often recover quickly from disturbance (e.g. Fritz & Dodds, 2004; Bogan *et al.*, 2014; Vander Vorste *et al.*, 2015), implying the existence of underlying processes promoting their resilience (i.e. ability to recover following disturbance; Stanley *et al.*, 1994). Among these processes, the colonization of previously disturbed habitats by drift (i.e. the active or passive downstream transport of organisms; Bilton, Freeland & Okamura, 2001) has been studied extensively (e.g. Needham, 1928; Müller, 1954; Townsend & Hildrew, 1976; Bruno, Bottazzi & Rossetti, 2012). Drift is a fundamental process of colonization in rivers (Brittain & Eikland, 1988; Mackay, 1992; Bilton *et al.*, 2001) that is driven by the dendritic nature of river networks and the overwhelming, unidirectional movement of water from upstream to downstream (Fagan, 2002; Altermatt, 2013). Today, it logically serves a predominant role in predictive models of community structure (e.g. Grant, 2011) and pervasive concepts in lotic ecology (e.g. Vannote *et al.*, 1980; Townsend, 1989; Poole, 2002).

Over the last two decades, other processes promoting community resilience in rivers have gradually been explored. For example, the vertical migration of organisms into the underlying hyporheic zone during disturbance (e.g. hyporheic refuge hypothesis; Palmer, Bely & Berg, 1992) and colonization of surface habitats from the hyporheic zone following disturbance are receiving growing interest (e.g. Dole-Olivier, 2011). The hyporheic zone is now viewed as a key component of riverscapes promoting community resilience, despite a paucity of empirical evidence (but see Holomuzki & Biggs, 2007; Kawanishi *et al.*, 2013). Aerial colonization is another process receiving great attention within lotic ecology following the recognition that community structure and composition are not only driven by local abiotic or biotic ecological processes but also by large-scale dispersal processes (Leibold *et al.*, 2004; Heino, 2013). Many aquatic invertebrates have an aerial stage which can promote colonization of previously disturbed habitats (Bilton *et al.*, 2001), making the topic of aerial dispersal abilities and its consequences for population and community dynamics a burgeoning field (e.g. Hughes, Schmidt & Finn, 2009; Cañedo-Argüelles *et al.*, 2015). Moreover, other processes, although less studied, can contribute to the resilience of rivers communities, such as the use of resistance forms (e.g. eggs, cysts, diapause; Stubbington & Datry, 2013) to survive during the disturbance, or the ability of some rheophilic organisms to migrate upstream (e.g. Bruno *et al.*, 2012). Together, results from these studies bring into question the paradigm that drift is the most important process promoting community resilience in rivers.

Alluvial rivers are widespread globally and represent ideal systems to explore the processes promoting resilience because they are frequently disturbed, inhabited by taxonomically rich and resilient

communities and provide multiple sources from which organisms can colonize previously disturbed channels (Arscott, Tockner & Ward, 2005; Tockner *et al.*, 2009). Alluvial rivers are frequently affected by natural flow disturbances, such as flooding (Doering *et al.*, 2007; Tockner *et al.*, 2009) and drying (Datry, 2012; Vander Vorste *et al.*, 2015). Yet alluvial river communities, notably aquatic invertebrates, are very resilient to these disturbances and generally recover in less than four weeks (e.g. Matthaei, Uehlinger & Frutiger *et al.*, 1997; Fowler, 2004; Vander Vorste *et al.*, 2015). High resilience is facilitated in alluvial rivers by the complex mosaic of habitats which can be used as refuges during disturbances and serve as sources of colonization afterwards (Arscott *et al.*, 2005; Stanford, Lorang & Hauer, 2005). For example, due to alternating bounded and unbounded sections of alluvial rivers, large-scale areas of upwelling and downwelling alternate longitudinally along the river corridor (e.g. Stanford & Ward, 1993, Capderrey *et al.*, 2013). Downwelling sections are prone to complete channel drying, while upwelling sections generally flow perennially (e.g. Doering *et al.*, 2007; Capderrey *et al.*, 2013), providing an important source of colonists (Malard *et al.*, 2002; Fowler, 2004; Vander Vorste *et al.*, 2015). Vertically, the expansive hyporheic zones found in alluvial rivers can provide more stable environmental conditions during floods and drying (e.g. Malard *et al.*, 2002, Dole-Olivier, 2011) and can harbour diverse invertebrate communities (e.g. Capderrey *et al.*, 2013) which may migrate to colonize the channel surface (e.g. Holomuzki & Biggs, 2007). Laterally, backwaters, riparian ponds and tributaries are also common aquatic habitats that are less prone to disturbance, hence constituting a source of aerial colonization for previously disturbed channels (Gray & Harding, 2007). The disturbance regimes of alluvial rivers and their mosaic of aquatic habitats provide a unique opportunity to manipulate potential sources of colonization and identify the primary processes that promote community resilience.

Our understanding of processes promoting community resilience in rivers has essentially been developed using small-scale experiments (e.g. Williams & Hynes, 1976; Palmer *et al.*, 1992), artificial channels and ponds (e.g. Ledger *et al.*, 2012; Boersma *et al.*, 2014) or field surveys (e.g. Fritz & Dodds, 2004; Datry *et al.*, 2014a; Vander Vorste *et al.*, 2015). These previous studies have been criticized for their inherent methodological limitations (Lake, 2000; Englund & Cooper, 2003). For example, the processes studied in small-scale experiments and artificial channels might not be relevant to large-scale flow disturbances, such as floods or drying (Englund & Cooper, 2003). Large-scale (e.g. river reaches) manipulative experiments permit replicability and manipulation at scales relevant to natural processes (Englund & Cooper, 2003); yet, they remain underutilized in lotic ecology (Larned *et al.* 2010) and virtually all such experiments have focused on floods (Olden *et al*., 2014). Therefore, large-scale manipulative experiments are needed to further explore the processes promoting community resilience after drying in rivers.

In this study, the view that drift is the primary process promoting invertebrate community resilience was challenged in an alluvial river using reach-scale flow manipulations. One-week drying

disturbances were generated in six channels, while three other channels that remained flowing were used as controls. Invertebrate community resilience was subsequently compared in channels with and without drift for four weeks after the drying event. Following the current paradigm in river ecology, we hypothesized that community structure and composition would be more severely affected by drying in the absence of drift. Therefore, we first predicted that blocking drift would lower taxonomic richness, density and evenness, and alter composition because of a dramatic reduction in the number of colonizers. We also hypothesized that communities recovering in channels without drift would differ in functional trait composition compared to those with drift. Thus, we predicted that blocking drift would dramatically lower functional trait richness, diversity and evenness, and alter trait composition because drifting taxa should provide a broad pool of biological traits for the colonization of previously disturbed channels. Lastly, we predicted that blocking drift would lower invertebrate body size in the channels because colonizers from the hyporheic zone, aerial oviposition and resistant forms tend to exhibit small body size.

4.3 Methods

4.3.1 River and study channels

The Eygues River is a main tributary to the Rhône River located in southern France (Figure 4.1). It is subject to a Mediterranean climate that induces frequent extreme flow events, including flooding and drying (Piégay *et al.*, 2009). The Eygues River catchment area is 1100 km² and it flows 114 km from its headwaters (1757 m a.s.l.) to the confluence with the Rhône near Orange (67 m a.s.l.).The Eygues River has a mean annual discharge of 6.22 $m^3 s^{-1}$ at the Pont-de-la-Tune gauging station (drainage area 473 km²) based on records from 1906–2003. As for most alluvial rivers in the region, it has an abundant bed load, erodible river banks and relatively steep slopes (Piégay *et al.*, 2009; Vander Vorste *et al.*, 2015). Near Nyons (62 km from the source), the Eygues River has an expansive 140-m wide alluvial floodplain, and flows across 3–4 channel braids. In this alluvial floodplain, nine channels with similar physical habitat characteristics (see *Physical characteristics*, Figure 4.1) were selected for the experiment along an 11 km section of the river.

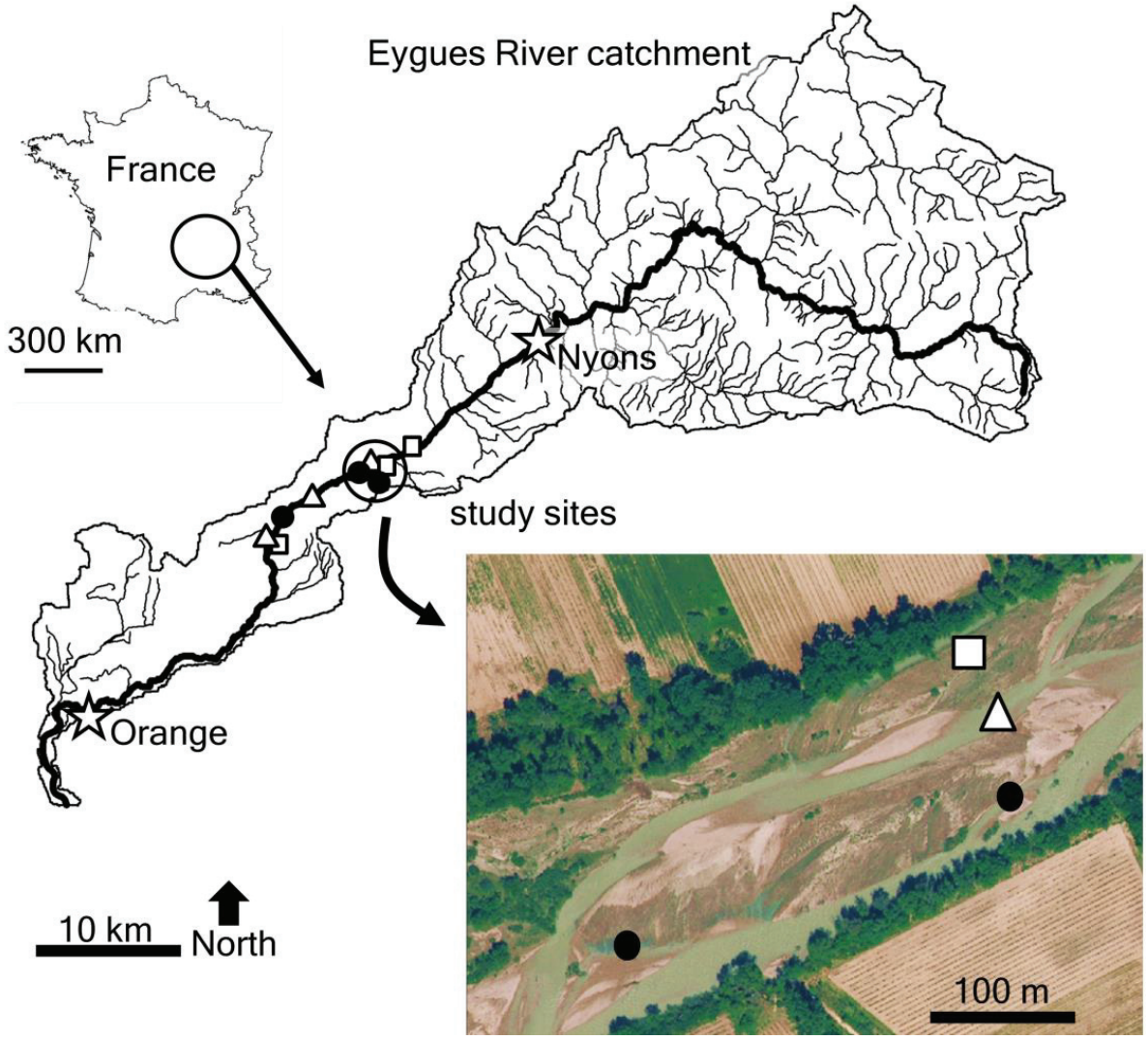

Figure 4.1 The Eygues River catchment and nine study channels in southeastern France with detailed view of four study channels (photo inset). Symbols represent the three treatment types: *Control* (●), *Drift* (Δ) and *NoDrift* (□).

4.3.2 The drying disturbance

Drying events (complete loss of surface water along the channel) were generated in six channels (52 ± 12 m length, 356 ± 97 cm wetted width) using dams constructed of plywood, tarpaulin and large boulders which diverted water from channels (Figure 4.2a). Dams were fixed across the channel width using steel stakes (1 m length), with care taken to minimize substratum disturbance during their installation (Figure 4.2b). After dam installation, channels dried within 24 hours and were kept dry for one week. Three *Control* channels (44 ± 11 m length, 505 ± 52 cm wetted width) were left undisturbed during the entire experiment.

4.3.3 Drift manipulation

After one week of drying, flow was re-established in the dried channels through four open gate valves in each dam (PVC tubes, 11 cm diameter; Figure 4.2b). In three of these six channels, drift was allowed through the valves (*Drift* treatment, Figure 4.2c). In the other three channels, drift was blocked by filtering water at each dam outlet using mesh drift nets (150 cm length, 250 µm mesh) attached to gate valves (11 cm diameter) fixed onto the PVC tubes (*NoDrift* treatment, Figure 4.2d). Invertebrates and organic matter that accumulated in drift nets were removed every 24 hours throughout the study period to prevent nets from clogging and to assess the potential contribution of drift (see *Sources of colonization*). During this time, individual gate valves were successively closed while the nets were removed and rinsed.

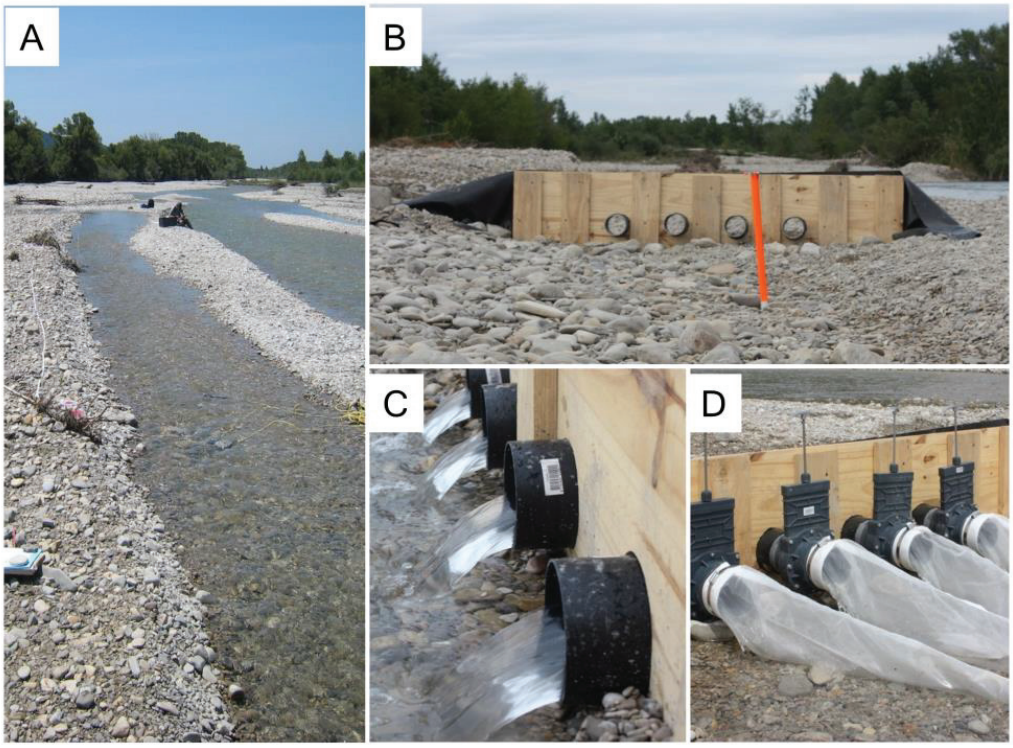

Figure 4.2 Alluvial river study channel (a). Dam used to divert water and create one-week drying event in *Drift* and *NoDrift* channels (b). Allowing invertebrate colonization by drift (*Drift*)(c). Blocking invertebrate colonization by drift using mesh drift nets (*NoDrift*)(d).

Sampling of invertebrates and physical characteristics that occurred before drying events are subsequently referred to as date *T0,* whereas sampling that occurred after one, two, three and four weeks of rewetting are distinguished by *T1–4*, respectively. Sampling that occurred on dates during the one-week drying events are referred to as dates *DryDay3,6,7*, where the numbers distinguish the specific sampling day.

4.3.4 Physical characteristics

Wetted width, water depth and discharge were measured at *T0* and *T1* to ensure similar physical characteristics were maintained in treatment channels following flow manipulations. Wetted width and water depth were measured at 10 locations along the length of each channel (Table 4.1). Discharge was estimated from depth and flow velocity measurements collected using a Flo-Mate current meter (Marsh McBirney, Loveland, Colorado; Table 4.1). To assess possible differences among channels that could influence colonization from the hyporheic zone and resistance forms, the following measurements were made: (i) water table depth measurements were taken on *DryDay7* by driving a stainless steel pipe (2 cm diameter, 14 cm long perforated area, 5 mm perforation diameter) into the riverbed until the water table was reached (Table 4.1); (ii) following rewetting at *T4*, vertical hydraulic gradient (VHG) and hydraulic conductivity (K) were measured at 10–20 locations each along the length of each channel using methods described by Datry *et al.*, 2014b (Table 4.1); (iii) median grain size (D_{50}) was estimated by randomly selecting and measuring 200 stones (coarse gravel–boulder, size range = -3.6 – -8.0 φ) from along the length of each channel (Table 4.1).

Table 4.1 Summary statistics of the physical characteristics measured in Control, Drift and NoDrift channels.

		Treatment Type		
		Control	Drift	NoDrift
Length (m)	mean ± 1 SD	44 ± 11	46 ± 20	58 ± 3
	min – max	60–65	13–60	55–60
Width (cm)	mean ± 1 SD	505 ± 72	392 ± 179	319 ± 15
	min – max	392–592	227–659	263–516
Depth (cm)	mean ± 1 SD	31 ± 2	12 ± 2	11 ± 5
	min – max	29–34	9–15	8–21
Q (m^3/s)	mean ± 1 SD	0.53 ± 0.25	0.05 ± 0.01	0.02 ± 0.03
	min – max	0.20–0.80	0.01–0.04	0.01–0.10
Water table depth (-cm)	mean ± 1 SD	–	36 ± 20	19 ± 9
	min – max	–	5–67	5–34
Vertical hydraulic gradient	mean ± 1 SD	-8.0 ± 2.6	-18.5 ± 11.9	-13.1 ± 3.9
	min – max	-6.1–11.0	-9.8–31.8	-9.7–17.3
Hydraulic conductivity (K)	mean ± 1 SD	$1.45\times10^{-5} \pm 6.61\times10^{-5}$	$2.59\times10^{-4} \pm 2.66\times10^{-4}$	$3.42\times10^{-4} \pm 9.89\times10^{-5}$
	min – max	$2.00\times10^{-4} – 3.23\times10^{-4}$	$8.99\times10^{-5} – 5.67\times10^{-4}$	$2.81\times10^{-4} – 4.56\times10^{-4}$
D50 (-phi)	mean ± 1 SD	4.6 ± 0.4	4.7 ± 0.3	4.8 ± 0.6
	min – max	4.5 – 5.0	4.5 – 5.0	4.5 – 5.0

4.3.5 Benthic invertebrate communities

Benthic invertebrates (BEN) were sampled from each channel on five sampling dates (*T0–4*). BEN samples were collected from four locations at equally-spaced locations (13 ± 3 m apart, mean ± 1 SD) along the length of the channel, using a Hess sampler (250 µm mesh, 0.125 m²) and preserved in 96% ethanol. Following *T1*, these locations were adjusted either upstream or downstream each week to avoid sampling the same location more than once during the study period.

4.3.6 Sources of colonization

The potential contribution of invertebrates in the hyporheic zone, those surviving in dry sediments using desiccation resistant forms, and those aerially ovipositing was assessed in *Drift* and *NoDrift* channels. Upon collection, all invertebrate samples were preserved in 96% ethanol. Hyporheic invertebrate (HYP) samples were collected at *DryDay7* from three equally-spaced locations (16 ± 4 m apart) along the length of each channel using methods detailed in Datry (2012). Briefly, a stainless steel standpipe (2 cm diameter, 14 cm long perforated area, 5 mm perforation diameter) was driven into the riverbed to a depth of 30 cm below the sediment surface with a sledge hammer. Six litres of water were then pumped from the hyporheic zone into a 12 L bucket using a Bou-Rouch pump, sieved through a 250 µm mesh net to retain invertebrates.

Taxa with desiccation-resistant forms in dry sediment (SED) were sampled at *DryDay7* from three equally-spaced locations along each channel, using methods detailed in Datry, Corti & Philippe (2012). At each location, 2.5 L of dry sediment was collected from a 0.25 m² area to a 5 cm depth using a hand-trowel. SED samples were taken to the laboratory ≤ 24 hours after collection, placed into 12 L plastic containers and inundated with 3 L of dechlorinated tap water. SED samples were aerated to maintain dissolved oxygen concentrations in the overlying water column close to saturation. Mesh lids (250 µm) were used to keep emerging and crawling invertebrates from escaping. At *T1*, following one week of inundation, invertebrates were collected by intensively stirring sediments by hand and pouring the sediment and water mixture into a mesh sieve (250 µm). The process was repeated five times until sediments had been thoroughly washed free of invertebrates.

Aerially ovipositing taxa (OVP) were sampled using sticky traps (1 m² total surface area) installed 0.5 m above the stream surface at three equally-spaced locations along each channel using methods described in Collier &Smith (1995). Sticky traps were coated on both sides (1 m² total surface area) with tree-pest adhesive. Sticky traps were deployed during the first week of rewetting (*T1* until *T2*) to minimize degradation/weathering of captured individuals. A petroleum based-solvent was used to remove invertebrates from the traps.

The potential contribution of drift was not assessed in *Drift* channels to avoid temporarily blocking colonization by drift. Instead, drifting invertebrates (DFT) were sampled from *NoDrift* channels over two 24 hour periods between *T1* and *T2*. The pre-installed drift nets were removed individually and invertebrates were washed from nets and preserved.

Invertebrates downstream of the dried channels were prevented from colonizing by upstream migration (Williams & Hynes, 1976) by scrubbing substratum located 1–2 m downstream by hand for 10 minutes between 1–3 times per day, washing invertebrates further downstream, throughout the study period.

4.3.7 Invertebrate processing and identification

Enumeration and identification of invertebrates was made to the lowest possible taxonomic level depending on their development and condition. Most aquatic insects were identified to genus- or species-level except for Chironomidae (Diptera), which were identified to subfamily. Most crustaceans, annelids and mites were identified either to the family, class or order. Adult insect taxa collected from OVP samples were counted, identified to family, sexed and the presence of gravid females was noted.

A total of 61 traits were used to explore community functional trait composition (Tachet *et al.*, 2002; Vander Vorste *et al.*, 2015). Traits comprised maximal size, life-cycle duration, potential number of reproductive cycles per year, aquatic stages, reproduction, dispersal mode and medium, resistance forms, respiration, locomotion and substrate relation, food and feeding style. The trait database used is fuzzy coded (scores 0–5) according to the affinity of each taxon to the particular trait (Tachet *et al.*, 2002). The relative proportion of taxa in a sample with each trait was then calculated by multiplying the proportional trait affinity scores by the $\log_{10}(x+1)$-transformed density and dividing this value by the total density per sample (Bonada et al. 2007).

From these traits, an *a priori* selection was made to further analyse potential differences in functional trait composition among treatments. *A priori* traits selection was made based on previous studies that found taxa with these traits dominated intermittent alluvial river communities (Bonada *et al.*, 2007; Datry *et al.*, 2014a; Vander Vorste *et al.*, 2015). Selected traits included: resistance forms (i.e. eggs, cocoons, desiccation-resistant cells, diapause/dormancy phase), small size (≤ 9 mm), tegument respiration and burrower-substrate relation.

Head capsule size (at the widest point), a surrogate of invertebrate body size (Fairchild & Holomuzki, 2005), was measured for 4794 invertebrates belonging to the genera *Baetis*, *Caenis*, *Leuctra*, *Ecdyonurus*, and *Simulini* and to the subfamilies Tanytarsini, Tanypodinae, Orthocladiinae. These eight taxa were the most common taxa in BEN samples, comprising > 90% of total density.

Measurements were made using an ocular micrometre to the nearest 0.1 mm. From the selected taxa, random subsampling (~10%) was used to select individuals for measurements when there were > 100 individuals per sample.

4.3.8 Data analysis

4.3.8.1 Differences in community structure and composition among treatments

To test our first hypothesis, community structure and composition among treatment types (3 levels: *Control*, *Drift*, *NoDrift*) and sampling dates (5 levels: *T0–4*) were compared using linear mixed effects (LME) models. These models tested for the effect of each factor and their interaction (i.e. whether the effect of treatment type depended on sampling date) on taxonomic richness, invertebrate density (ind m^{-2}) and Pielou's evenness. A nested, hierarchical approach was used to test for the effect of each factor, their interaction and select the most parsimonious model (Bolker *et al.*, 2009). First, a model was fitted, including treatment type, sampling date and the interaction term as fixed factors (i.e. full model). Second, subsequent models were constructed with a similar structure, removing one of the fixed factors (i.e. simple models). All models included random intercepts to account for random variance in metrics among the nine study channels. For example, full and simplified models for richness were coded as: full model (n = 166, d.f. = 17) = richness ~ treatment type + sampling date + treatment type:sampling date + (1|channel), simple model 1 (n = 166, d.f. = 9) = richness ~ treatment type + sampling date + (1|channel), simple model 2 (n = 166, d.f. = 5) = richness ~ treatment type + (1|channel), simple model 3 (n = 166, d.f. = 7) = richness ~ sampling date + (1|channel). Models were validated by plotting residuals against fitted values to check for violations of assumed normality and homogeneity. Subsequently, density and Pielou's evenness were $\log_{10}(x+1)$- and $\arcsin(\sqrt{x})$-transformed, respectively, to meet these assumptions. Third, likelihood ratio tests (χ^2) were used to determine the contribution of each fixed factor by comparing the fit (measured as deviance) between models with and without the factor (Bolker *et al.*, 2009). For example, the significance of the interaction term was assessed by comparing the full model to the model without interaction term (i.e. simple model 1). Akaike Information Criteria (AIC) were also used to select the most parsimonious model and improve interpretation of model comparisons beyond likelihood ratio tests (Bolker *et al.*, 2009). The AIC represent a model's goodness of fit and is adjusted based on the number of parameters included in the model (i.e. model complexity); the lower the AIC, the better the model fits the observed data (Bolker *et al.*, 2009). Once the best model was selected, *post hoc* comparisons of pairwise factor combinations were performed to identify differences between treatment types on specific sampling dates. All LME models were constructed and compared using the *lme4* package (Bates *et al.*, 2014) and pairwise *post hoc* comparisons were made using the *phia* package (De Rosario-Martinez, 2015) for R (R Development Core Team, 2011).

Adonis, a permutational multivariate analysis of variance (Anderson, 2001), was used to test the effect of treatment type, sampling date and their interaction on community composition. Adonis returns a R^2 statistic that is a measure of separation among treatment types (0 indicates complete mixing and 1 represents full separation) according to Bray–Curtis dissimilarity values, and a *P*-value estimated by repeated permutations (n = 999) of the data. Bray–Curtis dissimilarities were calculated using $\log_{10}(x+1)$-transformed invertebrate density, averaged within each channel for each sampling date. Non-metric multidimensional scaling (NMDS) was then used to visualize compositional changes in invertebrate communities among treatment types and sampling dates. Similarity percentages (SIMPER) analysis was used to identify taxa that contributed most greatly to the overall Bray–Curtis dissimilarity values. For taxa identified by SIMPER, LME models followed by *post hoc* comparison tests, as described above, were then used to test for the effects of treatment type, sampling date and their interaction on density. Adonis, NMDS and SIMPER analysis were performed with functions in the package *vegan* (Oksanen *et al.*, 2013) for R.

4.3.8.2 Differences in community functional trait composition among treatments

To test our second hypothesis, community functional trait composition among treatment types and sampling dates were compared using LME models followed by *post hoc* comparison tests. Functional trait richness, diversity and evenness were used as dependent variables in a similar nested, hierarchical approach as presented above. Functional trait richness was measured as the total number of traits present within the community. Functional diversity (i.e. Rao's quadratic entropy) was calculated as an abundance-weighted metric that measured the mean pairwise dissimilarities of randomly selected taxa in a community as a way of describing the breadth of traits present within each community (Rao, 1982, Botta-Dukát, 2005). Functional evenness was measured as the regularity of taxonomic density within the volume of different trait combinations present (Ricotta, Bacaro & Moretti, 2014). To meet model assumptions functional diversity and evenness were $\log_{10}(x)$- and $\arcsin(\sqrt{x})$-transformed, respectively. Functional trait richness, diversity and evenness were calculated using the packages *vegan*, *ade4* (Dray & Dufour, 2007) and the function *FeveR* (Ricotta *et al.*, 2014) for R, respectively.

Principal components analysis (PCA) was used to visualize differences among treatment types and sampling dates in the relative proportion of the four *a priori* selected traits (i.e. resistance forms, small size, tegument respiration and burrower substrate relation). LME models followed by *post hoc* comparison tests were used to test the effect of treatment type, sampling date and their interaction on the relative proportion of individual functional traits. The proportion of taxa in the sample with each functional trait was calculated based on taxon affinity for each trait (i.e. fuzzy coding) using the *ade4* (Dray & Dufour, 2007) for R.

To explore how the depth to the water table during drying events influenced community structural and functional resilience, correlation analyses were performed between water table depth and community

resilience. Community resilience in *Drift* and *NoDrift* channels was calculated as the number of weeks of rewetting required before mean values of taxonomic and functional metrics were not different or exceeded those of *Control* channels. This calculation yielded a total of five data points that ranged from 1–4 weeks in the time to recover from disturbance. Spearman rho, a nonparametric test for correlation, was then used due to the limited amount of data.

4.3.8.3 Differences in invertebrate size among treatments

LME models followed by *post hoc* comparison tests were used to test the effect of treatment type, sampling date (only *T0,1,4*) and their interaction on $\log_{10}(x+1)$-transformed mean head capsule width.

4.4 Results

4.4.1 Invertebrate richness and density

A total of 67 327 invertebrates representing 137 taxa was collected in BEN samples (n = 166) and a mean density of 7 889 ± 5 845 ind m^{-2} (mean ± 1 SD) from *Control*, *Drift* and *NoDrift* channels (Appendix S1). *Baetis*, *Caenis*, *Leuctra*, *Ecdyonurus* and *Simulini,* and the Chironomidae subfamilies Tanytarsini, Tanypodinae, Orthocladiinae were the most common BEN taxa. Among the sources of colonization sampled, HYP samples (n = 18) had 37 taxa with mean taxonomic richness of 10 ± 5 taxa and density of 97 ± 101 ind/6L (Appendix S1). SED samples (n = 18) had 16 taxa with mean taxonomic richness of 6 ± 2 taxa and density of 12 ± 26 ind m^{-2} (Appendix S1). OVP samples (n = 18) had 11 taxa with mean taxonomic richness of 2 ± 1 taxa and density of 4 ± 3 ind m^{-2} (Appendix S1). Gravid adult females comprised <10% of taxa captured in OVP samples. DFT samples (n = 6) had 67 taxa with a mean richness of 38 ± 6 taxa and density of 87 ± 63 ind $100m^{-3}$ (Appendix 4.1).

4.4.2 Differences in community structure and composition among treatments

There was a significant interaction between treatment type and sampling date for taxonomic richness (LME treatment × date: χ^2 (8 d.f.) = 27.026, $P < 0.001$), indicating that the temporal variation in taxonomic richness differed among treatments (Table 4.2, Figure 4.3). Before generating the disturbance (*T0*), there were no differences in taxonomic richness, among treatments (*post hoc* tests, $P > 0.05$, Figure 4.3). After one week of rewetting (*T1*), taxonomic richness was higher in *Control* versus *Drift* (*post hoc*: χ^2 (1 d.f.) = 5.65, P = 0.017) and *Control* versus *NoDrift* (*post hoc*: χ^2 (1 d.f.) = 4.13, P = 0.042), but there was no difference between the *Drift* versus *NoDrift* channels (*post hoc* tests, $P > 0.05$; Figure 4.3). After two weeks of rewetting (*T2*), taxonomic richness was no longer different among treatments (*post hoc* tests, $P > 0.05$; Figure 4.3). Density and Pielou's evenness did not differ among treatments on any sampling date (*post hoc* tests, $P > 0.05$, Figure 4.3). For all

treatments, density increased during the two-week period following rewetting (*T1* and *T2)*, before declining at *T3* and *T4* (Table 4.2, Figure 4.3). Pielou's evenness increased gradually following rewetting (LME date: χ^2 (12 d.f.) = 47.77, $P < 0.001$) (Table 4.2, Figure 4.3).

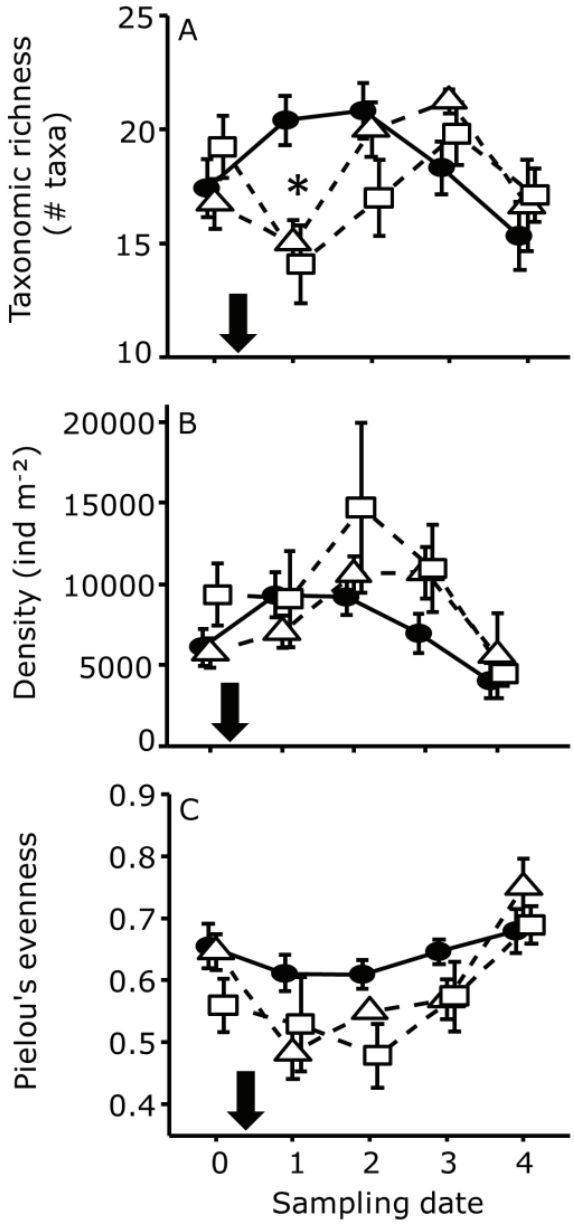

Figure 4.3 Differences in taxonomic richness (# of taxa) (A), density (ind m^{-2}) (B) and Pielou's evenness (C) among *Control* (●), *Drift* (Δ) and *NoDrift* (□) channels over the study period. Arrow indicates a one-week drying event between *T0* and *T1*. Error bars represent ±1 SE.

Table 4.2 Results of linear mixed effects models used to test the effect of treatment type (3 levels: *Control*, *Drift*, *NoDrift*), sampling date (5 levels: *T0–4* or 3 levels: *T0*, *1*, *4* for individual size) and their interaction on taxonomic structure, community function and individual size.

Metric Type	Factor	d.f.	ΔAIC	χ^2	*P*-value
Taxonomic structure					
	Richness				
	sampling date	12	17.15	41.15	<0.001
	treatment type	10	7.55	27.55	0.002
	sampling date × treatment type	8	11.02	27.03	<0.001
	Density				
	sampling date	12	25.77	49.77	<0.001
	treatment type	10	-11.00	9.00	0.532
	sampling date × treatment type	8	-7.12	8.88	0.352
	Evenness				
	sampling date	12	-23.77	47.77	<0.001
	treatment type	10	6.19	13.81	0.182
	sampling date × treatment type	8	3.45	12.55	0.128
Community function					
	Trait richness				
	sampling date	12	-23.40	47.39	<0.001
	treatment type	10	-13.57	33.56	<0.001
	sampling date × treatment type	8	-10.23	26.23	<0.001
	Diversity				
	sampling date	12	52.877	76.88	<0.001
	treatment type	10	6.417	13.59	0.193
	sampling date × treatment type	8	4.645	11.36	0.182
	Evenness				
	sampling date	12	8.59	32.59	0.001
	treatment type	10	-8.51	11.48	0.321
	sampling date × treatment type	8	-5.01	10.99	0.202
Individual size					
	Head capsule width				
	sampling date	6	9.12	21.12	0.002
	treatment type	6	7.19	19.19	0.004
	sampling date × treatment type	4	4.38	12.38	0.015

Community composition differed among treatments consistently across all sampling dates (adonis treatment × date: $R^2 = 0.096$, $P = 0.738$; Table 4.3, Figure 4.4). NMDS showed that before the disturbance (*T0*), there was little difference among treatments, but after one week of rewetting (*T1*), composition in *Control* differed from that of *Drift* and *NoDrift* channels, but *Drift* and *NoDrift* channels did not differ from each other (Figure 4.4). Composition became more similar over the sampling period until *T4*. Dissimilarity in community composition among treatment types was mainly

due to densities of *Baetis*, *Caenis* and *Leuctra*. The cumulative contribution of these taxa to dissimilarity was 15% for both *Drift* versus *NoDrift* and *Drift* versus *Control* and 18% for *NoDrift* versus *Control*. For *Baetis* density increased in *Control* channels from 250 ± 135 ind m^{-2} to 1220 ± 376 ind m^{-2} between *T0* and *T1* compared to *Drift* and *NoDrift* channels (LME treatment × date: χ^2 (8 d.f.) = 29.09, $P < 0.001$); however, at *T2*, densities of *Baetis* were no longer different among treatments (*post hoc* tests, $P > 0.05$).

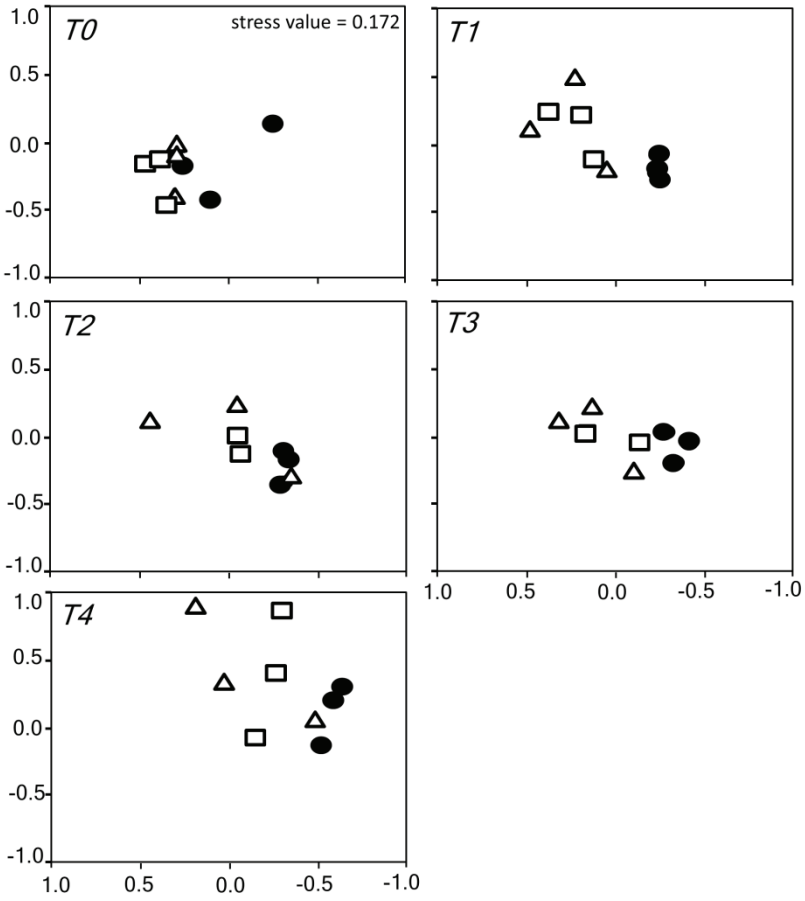

Figure 4.4 Differences in taxonomic richness (# of taxa) (A), density (ind m^{-2}) (B) and Pielou's evenness (C) among *Control* (●), *Drift* (Δ) and *NoDrift* (□) channels over the study period. Arrow indicates a one-week drying event between *T0* and *T1*. Error bars represent ±1 SE.

Table 4.3 Results from adonis testing the effect of treatment type (3 levels: *Control*, *Drift*, *NoDrift*), sampling date (5 levels: *T0–4*) and their interaction on community composition using Bray–Curtis dissimilarity values.

Source	d.f.	*F* statistic	R^2	*P*-value
sampling date	4	4.606	0.294	<0.001
treatment type	2	5.093	0.163	<0.001
sampling date × treatment type	8	0.754	0.096	0.738
residuals	28		0.447	
total	42		1.000	

4.4.3 Differences in community functional trait composition among treatments

There was a significant interaction between treatment type and sampling date for functional trait richness (LME treatment × date: χ^2 (8 d.f.) = 26.23, $P < 0.001$), indicating that the temporal variation in trait richness differed among treatments (Table 4.2, Figure 4.5). Before generating the disturbance (*T0*), there were no differences in trait richness among treatments (*post hoc* tests, $P > 0.05$, Figure 4.5). After one week of rewetting (*T1*), *Drift* and *NoDrift* differed from *Control* channels (*post hoc*: χ^2 (1 d.f.) = 27.10, $P < 0.001$, χ^2 (1 d.f.) = 16.89, $P < 0.001$, respectively), but not from each other. Trait richness increased in *Control* channels (35.5 ± 2.2 to 38.0 ± 1.3), but remained similar in *Drift* (34.6 ± 1.9 to 33.3 ± 2.6) and *NoDrift* channels (34.3 ± 1.5 to 34.3 ± 2.8) between *T1* and *T2*. All treatments showed similar patterns of functional diversity (LME sampling date: χ^2 (12 d.f.) = 76.88, $P < 0.001$) and functional evenness (LME sampling date: χ^2 (12 d.f.) = 32.59, $P = 0.001$) during the study period (Table 4.2, Figure 4.5).

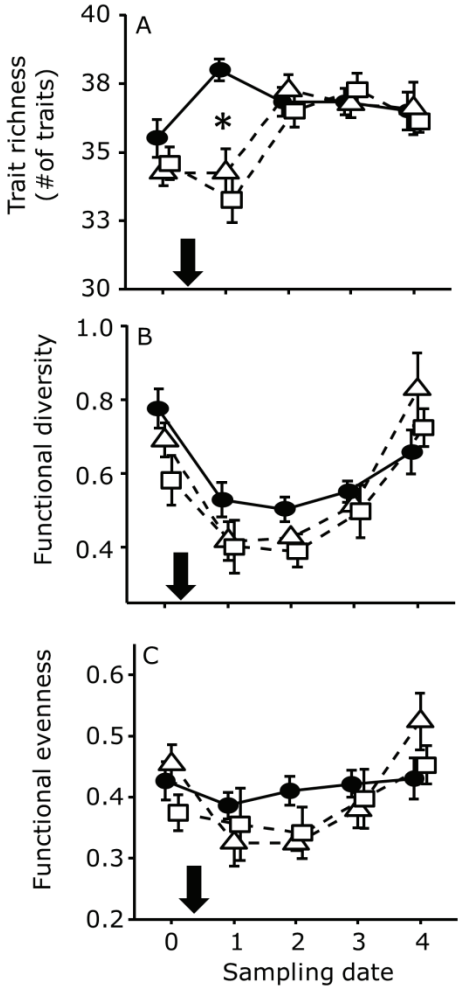

Figure 4.5 Differences in functional trait richness (A), diversity (B) and evenness (C) among *Control* (●), *Drift* (Δ) and *NoDrift* (□) channels over the study period. Arrow indicates a one-week drying event between *T0* and *T1*. Error bars represent ±1 SE.

Communities differed based in their relative proportion of the *a priori* selected traits (Figure 4.6). PCA showed that cross sampling dates, treatments were separated along axis 1 (66% of variability), indicating *Drift* and *NoDrift* had a higher proportion of taxa with small body size while *Control* channels had higher proportions of taxa with resistance forms (Figure 4.6). Temporal variability was different among treatments for both the proportion of small taxa (LME treatment × date: ΔAIC = 0.20, χ^2 (8 d.f.) = 16.21, P = 0.040) and resistance forms (LME treatment × date: ΔAIC = 4.02, χ^2 (8 d.f.) = 2.08, P = 0.010). At *T0*, the proportion of small taxa was not different for *Drift* versus *NoDrift* (*post hoc* tests: P > 0.05), but both treatment types had a significantly higher proportion than *Control* channels (*post hoc*: χ^2 (1 d.f.) = 6.16, P = 0.013, χ^2 (1 d.f.) = 5.47, P = 0.019, respectively). These differences persisted until *T4* for *Control* versus *Drift* and at *T2* for *Control* versus *NoDrift* (*post hoc* tests, P > 0.05).

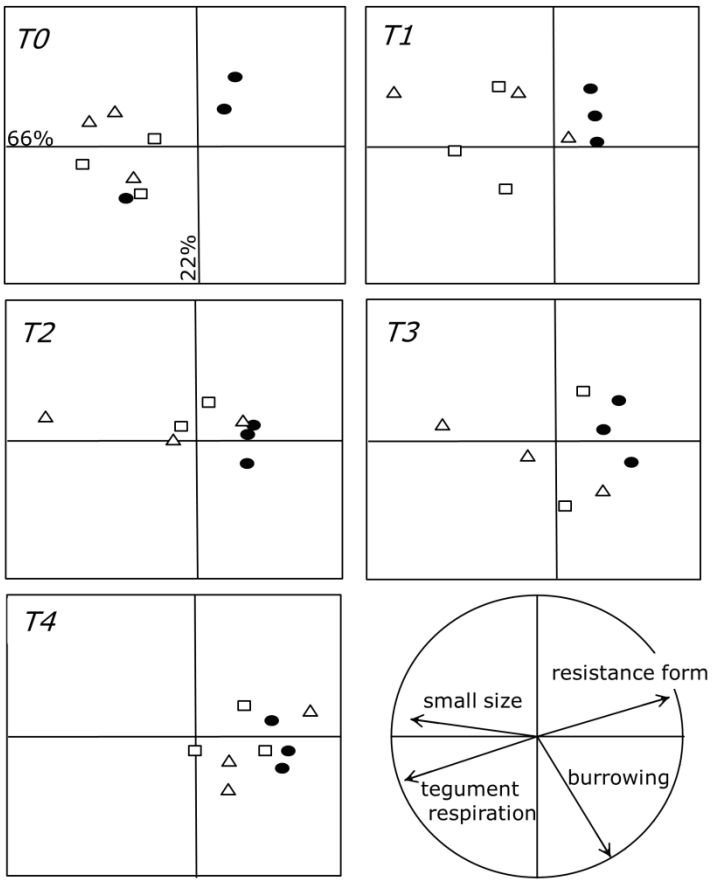

Figure 4.6 Principal components analysis (PCA) showing differences among channels in the relative proportion of taxa with small size (≤ 9 mm), tegument respiration, resistance forms and burrowing habit among *Control* (●), *Drift* (Δ) and *NoDrift* (□) over the sampling period. A one-week drying event occurred between *T0* and *T1* sampling dates.

Resilience of community taxonomic richness (Spearman rho test: rho = 0.866, $P = 0.058$) and functional diversity (Spearman rho test: rho = 0.949, $P = 0.014$) in *Drift* and *NoDrift* was positively correlated with mean depth to the water table during drying events (Figure 4.7). Resilience of density, evenness, functional trait richness and evenness were not correlated with water table depth (Spearman rho tests: $P > 0.05$).

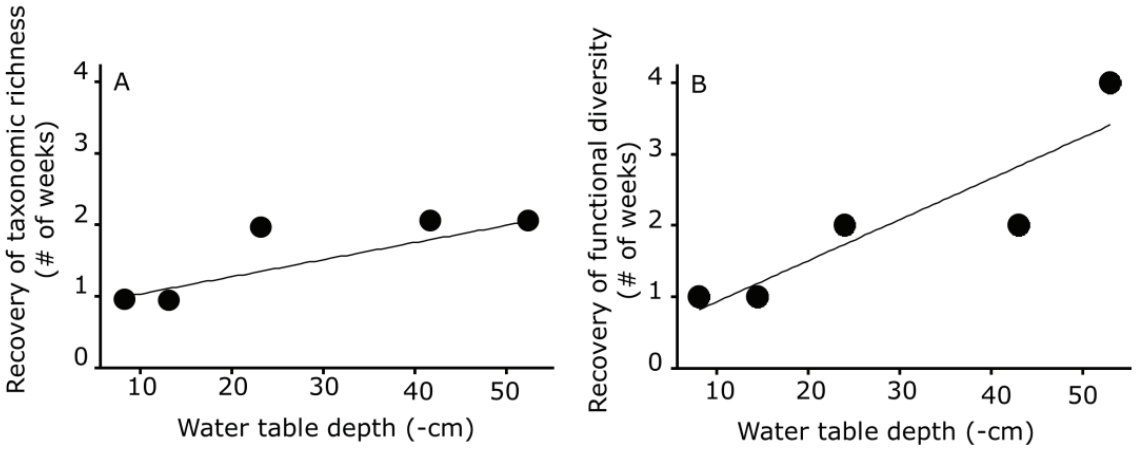

Figure 4.7 Relationship between recovery of taxonomic richness and functional diversity and the mean water table depth in channels during drying (-cm). Correlation tested with Spearman rho test (rho = 0.866, $P = 0.058$ for taxonomic richness, rho = 0.949, $P = 0.014$ for functional diversity).

4.4.4 Differences in invertebrate size among treatments

There was a significant interaction of treatment type and sampling date on mean head capsule size of the eight most common taxa (LME treatment × date: χ^2 (4 d.f.) = 12.38, $P = 0.015$), indicating that the temporal variation in size differed among treatments (Table 4.2, Figure 4.8). Before the drying event (*T0*), there was no difference in size among treatments (*post hoc* tests, $P > 0.05$). Upon one week of rewetting (*T1*), size decreased significantly compared to *Control* in both *Drift* and *NoDrift* channels (*post hoc*: χ^2 (1 d.f.) = 4.99, $P = 0.026$, χ^2 (1 d.f.) = 7.70, $P = 0.006$, respectively) and remained smaller until *T4* (*post hoc*: χ^2 (1 d.f.) = 6.31, $P = 0.012$, χ^2 (1 d.f.) = 9.31, $P = 0.002$, respectively).

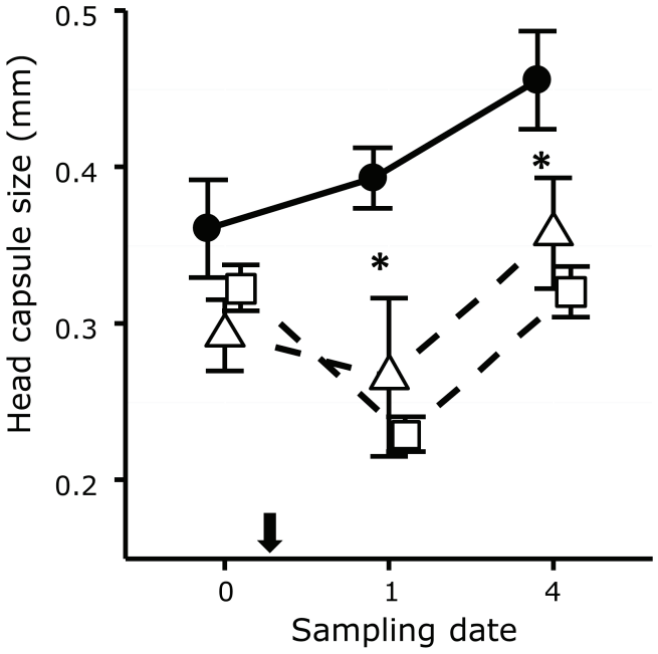

Figure 4.8 Mean head capsule size (mm) of the eight most abundant invertebrate taxa among *Control* (●), *Drift* (Δ) and *NoDrift* (□) channels. Arrow indicates a one-week drying event between *T0* and *T1*. Error bars represent ±1 SE.

4.5 Discussion

4.5.1 Drift is not the primary process promoting the resilience of invertebrate communities

In the Eygues River, the view that drift is the primary process of invertebrate colonization (Brittain & Eikland, 1988; Mackay, 1992; Bilton *et al.*, 2001; Altermatt, 2013) was challenged. Contradictory to our hypothesis based on this view, invertebrate communities were similarly affected by drying in channels without colonization by drifting invertebrates, as the resilience of community structure and composition was as high when drift was blocked. Furthermore, our hypothesis that functional trait composition would be more altered by drying in the absence of drift was unsupported. Against our predictions, community functional trait richness, diversity and evenness were similar in channels with and without drift and parallel shifts in invertebrate size following rewetting suggest sources of colonists were similar across dried channels. These results contrast with many previous studies supporting the "drift paradigm" in small-scale experiments (e.g. Townsend & Hildrew, 1976; Williams & Hynes, 1976; Palmer *et al.*, 1992; Bruno *et al.*, 2012) or observational field studies (e.g. Matthaei *et al.*, 1997) and suggest that drift may not be of overwhelming importance in promoting high community resilience, including the recovery of functional aspects of communities, in intermittent alluvial rivers.

In this alluvial river, invertebrate communities were highly resilient to drying, both structurally and functionally after a one-week drying event. Taxonomic richness, density and evenness all recovered within one to two weeks of rewetting. Previous studies in alluvial rivers in New Zealand, Switzerland and France have also found high community resilience to both floods (e.g. Sagar, 1986; Matthaei *et al.*, 1997) and longer drying events than generated in this study (e.g. Fowler, 2004; Vander Vorste *et al.*, 2015), with recovery generally occurring in less than four weeks following disturbance. Functional diversity was not different in dried channels compared to control channels in this study, despite lower taxonomic and functional trait richness after one week of rewetting. This supports the idea that communities in disturbed environments are functionally redundant (i.e. distinct taxa have similar functional traits) because harsh environmental conditions may exclude taxa that are poorly adapted to these conditions, yielding communities comprised of disturbance-resistant and/or resilient taxa (Mouchet *et al.*, 2010; Boersma *et al.*, 2014; Vander Vorste *et al.*, 2015). In the Eygues River, recovery of the eight most common taxa, comprising 90% of total density, within one to two weeks of rewetting, was likely the most important reason for high functional resilience. For example, the most common taxa, *Baetis* spp., reached densities up to 470 ind m^{-2} after one week of rewetting. This genus has a small body size, strong swimming ability and can disperse aerially as an adult and, therefore, could potentially colonize previously disturbed channels by drift, vertical migration from the hyporheic zone, aerial oviposition or any combination of these processes.

In alluvial rivers, high resilience of communities can also be explained by the availability of multiple sources of colonization that are generated through habitat-mosaic dynamics and found vertically, longitudinally and laterally from disturbed channels (Malard *et al.*, 2002; Arscott *et al.*, 2005; Stanford *et al.*, 2005). This three-dimensional matrix of colonization sources allows organisms to colonize using multiple processes (i.e. pathways *sensu* Grant *et al.*, 2010), increasing community resilience (Fagan, 2002; Grant, 2011). For example, the persistence of modelled river communities facing disturbances were previously shown to be strongly related to the number of colonization sources and their spatial arrangement on the landscape (e.g. Fagan, 2002; Grant, 2011). In these studies, resilience of communities increased greatly when the number of sources increased and colonization occurred from multiple pathways. Furthermore, this dimensionality implies that resilience can be maintained despite the loss of a potential colonization process (e.g. drift), if other colonization sources remain and taxa have traits that facilitate their use (e.g. vertical migration, aerial oviposition, resistance forms). Identifying and quantifying these sources and processes has been identified as a key challenge facing ecologists aiming to explain patterns in community dynamics (Nathan, 2001), hence the demand for empirical evidence (Grant, 2011).

4.5.2 Is vertical migration from the hyporheic zone an essential process promoting invertebrate community resilience?

Three lines of evidence indicate the hyporheic zone was the main source of colonists upon rewetting. First, the hyporheic zone contained, during the drying event, all eight of the most common taxa found in the benthic zone. Second, there was a distinct decrease in head capsule width, a measure of body size, of the eight most common taxa upon rewetting in all treatment channels. This suggests that taxa were coming from the hyporheic zone, where body size is arguably the most important attribute limiting invertebrate colonization (Gayraud & Philippe, 2001; Bo *et al.*, 2006; Navel *et al*., 2010; Descloux, Datry & Usseglio-Polatera, 2014). Third, community resilience was negatively correlated with the depth of the water table during drying: the recovery time of both taxonomic richness and functional diversity increased as the water table depth increased. This circumstantial evidence, together with finding that blocking drift had no effect on invertebrate community resilience, indicates most taxa colonizing the rewetted channels originated from the hyporheic zone. Previous studies have suggested that the hyporheic zone could be a source of colonists following disturbance in alluvial rivers (e.g. Holomuzki & Biggs, 2007; Kawanishi *et al.*, 2013). For example, Holomuzki & Biggs (2007) found densities of the snail *Potamopyrgus antipodarum* recovered within 12 to 24 hours of floods because it used the hyporheic zone as a refuge to escape the strong hydraulic forces. However, further experiments are still needed to deduce direct evidence of the hyporheic refuge hypothesis (i.e. organisms enter the hyporheic zone during disturbance and then return to the surface; Palmer et al. 1992, Stubbington, Wood & Reid, 2011, Dole-Olivier 2011). In this experiment, it was not possible to distinguish if organisms collected following rewetting were also in the benthic zone prior to drying, or if they had already been in the hyporheic zone as eggs or early instars. Future mark-recapture or mesocosm experiments could be used to address this distinction. For example, Kawanishi *et al.* (2013) recaptured individuals of the benthic fish, *Cobitis shikokuensis*, in an intermittent alluvial river after they were collected from the hyporheic zone beneath the dried channel. Combined with the results from this study, there is mounting evidence that the vertical migration of organisms from the hyporheic zone can be an essential processes promoting resilience in alluvial rivers.

Alluvial rivers, such as the Eygues River, are common across most of the Alps and other European mountain ranges including the Apennines and Pyrenees (Piégay *et al.*, 2009; Tockner *et al.*, 2009). These rivers also stretch across large portions of the western United States, Canada, Alaska and New Zealand (Stanford *et al.*, 2005; Gray & Harding, 2007). However, generalizing these results across all alluvial rivers or other river types should be done with caution because the hydrological connections between surface and hyporheic habitats are known to vary spatially along the river corridor (Stanford & Ward, 1993; Malard *et al.*, 2002; Stubbington et al., 2011). For example, in alluvial rivers where the hyporheic zone is unsaturated during dry periods, it is unlikely that its contribution to community

resilience would be high (e.g. Datry, 2012). In the Eygues River, channels featured relatively large grain size, high porosity and shallow depth of the water, hence providing an ideal setting to assess the importance of the hyporheic zone as a source of colonization for surface communities. Yet these channel features are not exclusive to alluvial rivers, and the importance of the hyporheic zone as a refuge and/or source has been evoked across many river types (Williams & Hynes, 1976; Boulton *et al.*, 1992; Stubbington *et al.*, 2015). Therefore, the importance of the hyporheic zone to community resilience may hold true in other river systems as well.

Resistance forms and aerial oviposition may not be as important for promoting community resilience in alluvial rivers as in other systems. In this study, only 7% of benthic taxa were found in dry sediments and density of these taxa was very low (12 ± 26 ind m^{-2}). In contrast, Storey & Quinn (2013) found dry sediments contained 70% of the taxa from nearby flowing headwater streams in New Zealand. Similarly, Datry *et al.* (2012) recovered 65% of the benthic taxa in the Albarine River from dry river sediments. In alluvial rivers, coarse, dry sediments may not maintain the high relative humidity generally associated with invertebrate seedbank viability (Storey & Quinn, 2013; Stubbington & Datry, 2013). Only 10% of benthic taxa of adult insects were collected from sticky traps in this study suggesting aerial oviposition was not an important process promoting resilience following rewetting (≤ 4 weeks) in this river. In contrast, previous studies have shown aerial oviposition can be a key process of colonization in spatially isolated systems such as headwater (e.g. Hughes, Schmidt & Finn, 2009) and arid-land streams (e.g. Cañedo-Argüelles *et al.*, 2015), where long distances from colonization sources are only overcome by taxa with strong flight capabilities.

Despite strong circumstantial evidence, future experiments are needed to demonstrate and quantify the contribution of the hyporheic zone to community resilience. Reach-scale field experiments that manipulate the vertical migration of organisms, using either artificial (e.g. nylon mesh) or natural barriers (e.g. fine sediments), could provide direct evidence of the importance of this process for community resilience. These experiments should be performed across a gradient of stream sizes and types to improve the generality of findings. Clearly, physical habitat characteristics (e.g. % fine sediment, porosity and hydraulic conductivity) affect the vertical migration of organisms (Navel *et al.*, 2010; Descloux *et al.*, 2014; Vadher, Stubbington & Wood, 2015). Yet other abiotic (e.g. water temperature) and biotic (e.g. intraspecific competition) factors could also play an important role (Stubbington *et al.,* 2011).

4.5.3 Considering and managing habitat connectivity in three-dimensions

Drift has often been viewed as the primary process promoting the resilience of invertebrate communities in rivers (e.g. Townsend & Hildrew, 1976; Williams & Hynes, 1976; Brittain & Eikland, 1988; Mackay, 1992; Bilton *et al.*, 2001) and unidirectionality (longitudinal) is a pervasive concept in

lotic ecology (Poole, 2002; Fagan, 2002). However, the results of this study indicate that a three-dimensional perspective is more appropriate, at least for alluvial rivers. While the lateral dimension of river ecosystems has long been recognized in basic and applied research, the vertical dimension tends to be overlooked, notably in management practices (Boulton *et al.*, 2010). The hyporheic zone is threatened by many human activities, including agriculture, mining and flow regulation that lead to its clogging with fine sediments (Datry *et al.*, 2014b) and limiting the vertical migration of organisms (Navel *et al*., 2010; Descloux *et al.*, 2014; Vadher *et al.*, 2015). Furthermore, climate change, water abstraction and flow regime alterations can increase the severity of drying events in rivers (Larned *at al.*, 2010), lowering the water table and preventing the use of the hyporheic zone as a refuge by invertebrates (e.g. Clinton, Grimm & Fisher, 1996). In a context of increasing pressures on river ecosystems, adaptable management approaches are needed to direct attention to sources (e.g. hyporheic zone) that are essential to promoting community resilience (Palmer *et al.*, 2005; Heino, 2013).

4.6 Acknowledgments

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Appendix 4.1 Invertebrate taxa collected in benthic invertebrate (BEN), drifting invertebrate (DFT), hyporheic zone invertebrate (HYP), aerially ovipositing invertebrate (OVP), desiccation resistant forms in dry sediment (SED) sampling efforts. Relative abundance (RA) calculated as mean relative abundance per sample. Frequency of occurrence (FO) calculated as proportion of samples a taxon was present.

	BEN $_{Control}$						**BEN $_{Drift}$**						**BEN $_{NoDrift}$**						**DFT**	**HYP**	**OVP**	**SED**
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Plecoptera	0	0	0	0	0	0	0	0.2	0	1	0	4	0	0	0	0	0	0				
Leuctra	25.6	24.3	0	89	7	97	0.5	0.5	0	1	3	52	7.6	19.2	0	129	2	60	X	X		
Nemouridae	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0.2	0	1	0	4				
Protonemura	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Nemoura	0.1	0.6	0	4	0	7	0.1	0.2	0	1	0	6	0.1	0.3	0	2	0	4	X			
Perlidae	0.1	0.3	0	2	0	3	0	0	0	0	0	0	0	0	0	0	0	0	X			
Perla	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Perlodidae	0.3	0.7	0	4	0	18	0.1	0.3	0	1	1	13	0.2	0.6	0	3	0	8	X	X		
Isoperla	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0			X	
Trichoptera	0	0.1	0	1	0	2	0	0.2	0	1	0	4	0	0.1	0	1	0	2	X	X	X	
Hydropsychidae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Cheumatopsyche lepida	0.1	0.3	0	2	0	7	0	0	0	0	0	0	0	0	0	0	0	0				
Hydropsyche	8.0	11.2	0	58	3	80	0.2	0.4	0	1	1	20	2.2	4.5	0	28	1	48	X			
Hydropsyche dinarica	0.1	0.4	0	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0				

	BEN Control						BEN Drift						BEN NoDrift						DFT	HYP	OVP	SED
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Hydropsyche exocellata	0.2	0.6	0	3	0	10	0	0	0	0	0	0	0	0	0	0	0	0				
Hydropsyche incognita	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0				
Hydropsyche modesta	0	0.2	0	1	0	3	0	0.2	0	1	0	4	0	0.2	0	1	0	4				
Hydropsyche pellucidula	0.1	0.5	0	4	0	3	0	0	0	0	0	0	0	0	0	0	0	0				
Hydroptilidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Agraylea	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	1	0	2				
Hydroptila	0.2	0.5	0	2	0	18	0.1	0.3	0	1	0	7	0.2	0.7	0	4	0	15	X			
Oxyethira	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0.2	0	1	0	4				
Leptoceridae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Athripsodes	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0				
Phryganeidae	0.1	0.5	0	4	0	5	0	0	0	0	0	0	0	0.1	0	1	0	2				
Polycentropodidae	0	0.2	0	1	0	3	0	0.2	0	1	0	4	0	0	0	0	0	0				
Holocentropus	0.1	0.2	0	1	0	5	0	0	0	0	0	0	0	0	0	0	0	0				
Plectrocnemia	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Rhyacophila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Sericostomatidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Ephemeroptera	0.1	0.7	0	5	0	5	0	0	0	0	0	0	0	0	0	0	0	0		X	X	

	BEN Control						BEN Drift						BEN NoDrift						DFT	HYP	OVP	SED
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Baetidae	0	0	0	0	0	0	0	0.1	0	1	0	2	1.1	5.7	0	36	0	6	X	X	X	
Ameletus	0.1	0.4	0	3	0	2	0.1	0.2	0	1	0	6	0	0	0	0	0	0				
Acentrella	1.7	3.9	0	25	0	42	0	0.2	0	1	0	4	0.3	1.7	0	11	0	8	X			
Baetis	118.6	103.5	0	390	32	97	0.9	0.3	0	1	6	91	109.6	176.9	0	749	20	75	X	X	X	
Centroptilum luteolum	0.8	3.6	0	19	0	7	0.3	0.4	0	1	1	26	2.4	6.1	0	27	1	23				
Procloeon pennulatum	0.9	2.8	0	17	0	22	0.4	0.5	0	1	3	44	3.3	8.1	0	39	2	37				
Procloeon bifidum	0.8	4.6	0	31	0	3	0.1	0.3	0	1	1	11	0.2	0.8	0	6	0	6	X			
Caenis	61.2	61.6	1	294	17	100	1.0	0.1	0	1	6	98	50.9	62.1	0	238	14	90	X	X	X	X
Ephemerella	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0		X		
Serratella ignita	0.2	0.6	0	3	0	12	0.2	0.4	0	1	1	17	0.3	1.0	0	6	0	12	X			
Potamanthus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			X	
Heptageniidae	1.3	5.7	0	36	0	10	0	0.2	0	1	0	4	1.4	4.6	0	25	0	15	X	X	X	
Electrogena	2.3	5.2	0	27	1	35	0.4	0.5	0	1	2	37	3.2	6.8	0	35	1	42				
Ecdyonurus	27.4	32.7	0	188	8	90	0.4	0.5	0	1	2	39	5.6	10.5	0	54	1	54	X			
Ecdyonurus aurantiacus	0	0.2	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	0				
Heptagenia	0.2	0.5	0	2	0	13	0	0.1	0	1	0	2	0.1	0.7	0	5	0	6				
Rhithrogena	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				

	BEN Control						BEN Drift						BEN NoDrift						DFT	HYP	OVP	SED
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Leptophlebiidae	0.2	0.7	0	3	0	12	0	0	0	0	0	0	0.1	0.2	0	1	0	6	X	X		
Paraleptophlebia	0.2	0.5	0	3	0	10	0.3	0.5	0	1	2	28	1.8	4.2	0	22	1	31				
Choroterpes picteti	4.0	6.7	0	31	1	53	0.2	0.4	0	1	1	20	1.2	2.6	0	12	0	35	X			
Habroleptoides	0.1	0.4	0	3	0	3	0	0	0	0	0	0	0	0.1	0	1	0	2				
Oligoneuriidae	0.2	1.5	0	12	0	2	0	0	0	0	0	0	0	0.3	0	2	0	2			X	
Oligoneuriella	1.4	3.2	0	16	0	32	0	0.2	0	1	0	4	0.4	2.0	0	13	0	8	X			
Ephoron	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Ephoron virgo	0	0.1	0	1	0	2	0	0.1	0	1	0	2	0	0.1	0	1	0	2	X			
Diptera	0	0.1	0	1	0	2	0.1	0.3	0	1	1	9	0.3	0.8	0	5	0	17		X		X
Atrichops crassipes	0	0.1	0	1	0	2	0	0.1	0	1	0	2	0	0	0	0	0	0				
Tanypodinae	5.2	6.8	0	40	2	83	0.9	0.3	0	1	6	93	16.0	38.3	0	276	5	88	X	X		X
Tanytarsini	22.4	39.6	0	228	6	92	1.0	0.1	0	1	6	98	82.3	90.4	0	400	24	98	X	X		X
Orthocladiinae	30.2	63.7	0	276	8	92	1.0	0.1	0	1	6	98	36.9	53.6	0	210	11	96	X	X		X
Chironomini	5.6	9.4	0	60	2	68	0.7	0.5	0	1	4	67	9.2	23.5	0	160	2	56	X	X		X
Prodiamesinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Diamesinae	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	1	0	2				
Chironomidae pupae	1.9	3.2	0	15	1	60	0.6	0.5	0	1	4	59	3.2	5.6	0	24	1	46		X		X
Chironomidae adult	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	1	0	2				X

	BEN Control						BEN Drift						BEN NoDrift						DFT	HYP	OVP	SED
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Ceratopogonidae	0.2	0.5	0	2	0	15	0.6	0.5	0	1	3	61	1.9	2.8	0	18	1	69	X	X		X
Ceratopogoninae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Dixa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Dolichopodidae	0	0	0	0	0	0	0.1	0.3	0	1	1	13	0.8	1.9	0	10	1	23				
Clinocerinae	0.1	0.3	0	2	0	3	0.1	0.2	0	1	0	6	0.1	0.2	0	1	0	6	X			
Hemerodromiinae	0.1	0.3	0	2	0	3	0.1	0.3	0	1	1	11	0.1	0.3	0	1	0	8				
Limoniidae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Eriopterini	0	0	0	0	0	0	0	0.2	0	1	0	4	0	0.1	0	1	0	2				
Tipulidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Hexatomini	0	0.2	0	1	0	3	0.1	0.3	0	1	1	9	0.1	0.6	0	4	0	4	X	X		
Hexatoma	2.8	3.0	0	13	1	70	0.7	0.5	0	1	4	69	3.5	3.5	0	16	1	88	X	X		
Psychodidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			X
Prosimulium larvae	0	0.1	0	1	0	2	0	0.1	0	1	0	2	0	0	0	0	0	0				
Simuliidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Simuliini larvae	18.2	26.1	0	88	7	82	0.3	0.5	0	1	2	33	12.1	45.0	0	307	2	52		X		
Simulium lineatum	0.3	1.8	0	14	0	3	0	0	0	0	0	0	0	0	0	0	0	0				
Simulium sp1	0.9	2.8	0	15	0	22	0	0.2	0	1	0	4	0.2	0.9	0	6	0	6				
Simulium sp2	0.2	0.6	0	4	0	12	0	0.1	0	1	0	2	0	0	0	0	0	0				

	BEN Control						BEN Drift						BEN NoDrift									
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**DFT**	**HYP**	**OVP**	**SED**
Simulium sp3	0	0.2	0	1	0	3	0	0.1	0	1	0	2	0	0	0	0	0	0				
Prosimuliini	0	0	0	0	0	0	0	0.1	0	1	0	2	1.0	7.5	0	54	0	2				
Simulium equinum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Stratiomyidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Tabanus	0	0.3	0	2	0	2	0	0.2	0	1	0	4	0.1	0.3	0	1	0	8	X			X
Tipulidae 1	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Hexatomini 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Hexatoma 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Tipula	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0.1	0	1	0	2				
Odonata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			X	
Calopteryx	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Corduliidae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Cordulegaster	0	0.1	0	1	0	2	0	0.1	0	1	0	2	0	0	0	0	0	0				
Gomphidae	0.7	1.4	0	8	0	33	0.3	0.5	0	1	1	30	0.4	0.8	0	3	0	23	X	X		
Onychogomphus	0.3	0.6	0	2	0	18	0.2	0.4	0	1	1	20	0.2	0.5	0	3	0	13	X			
Ophiogomphus	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0.1	0	1	0	2				
Coleoptera	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0		X		X
Dryops	0	0	0	0	0	0	0.1	0.3	0	1	0	9	0.1	0.4	0	2	0	8	X	X		

	BEN Control						BEN Drift						BEN NoDrift						DFT	HYP	OVP	SED
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Pomatinus	0	0.3	0	2	0	2	0	0.1	0	1	0	2	0	0	0	0	0	0	X			
Dytiscidae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Bidessus	0.2	1.0	0	6	0	7	0.1	0.2	0	1	0	6	0.3	0.7	0	3	0	13	X			
Deronectes	0	0	0	0	0	0	0	0	0	0	0	0	0	0.3	0	2	0	2	X			
Graptodytes	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Laccophilus	0	0.1	0	1	0	2	0	0.1	0	1	0	2	0	0.1	0	1	0	2				
Siettitia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		X		
Stictotarsus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Stictonectes	0	0	0	0	0	0	0	0.2	0	1	0	4	0.1	0.4	0	2	0	8				
Noterus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Hydroporinae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0.2	0	1	0	4				
Suphrodytes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Platambus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Hydroporus	0	0	0	0	0	0	0	0	0	0	0	0	0	0.2	0	1	0	4				
Nebrioporus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Stenelmis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Hydroglyphus	0.1	0.5	0	4	0	2	0	0	0	0	0	0	0.1	0.3	0	2	0	6		X		
Scarodytes	0.1	0.4	0	3	0	2	0.1	0.3	0	1	0	9	0.1	0.4	0	2	0	10	X			

	BEN Control						BEN Drift						BEN NoDrift									
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**DFT**	**HYP**	**OVP**	**SED**
Yola	0.2	0.5	0	3	0	12	0.1	0.3	0	1	0	9	0.1	0.2	0	1	0	6		X		
Dryops	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X			
Peltodytes	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0	X			
Helophorus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0				
Hydraenidae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0.1	0	1	0	2				
Elmidae	0.1	0.4	0	3	0	3	0.1	0.3	0	1	0	7	0	0.1	0	1	0	2				
Bythiospeum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		X		
Dupophilus	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Esolus	0.5	1.2	0	8	0	30	0	0.2	0	1	0	4	0.3	0.9	0	5	0	19	X			
Elmis	0.1	0.3	0	1	0	10	0	0	0	0	0	0	0	0	0	0	0	0	X			
Limnius	0.1	0.3	0	1	0	10	0.1	0.3	0	1	1	13	0.1	0.4	0	3	0	4	X			
Normandia	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0	X			
Macronychus	0.2	0.9	0	7	0	7	0.1	0.2	0	1	0	6	0.1	0.4	0	3	0	2				
Limnius/Macronychus	0	0	0	0	0	0	0	0.1	0	1	0	2	0.2	1.4	0	10	0	4				
Oulimnius	0.5	2.0	0	15	0	20	0.2	0.4	0	1	1	17	0.1	0.4	0	2	0	8	X			
Helophorus	0	0	0	0	0	0	0	0.2	0	1	0	4	0.1	0.3	0	2	0	6				
Ochthebius	0	0	0	0	0	0	0	0	0	0	0	0	0.3	1.9	0	14	0	2	X			
Hydrophilidae	0	0.1	0	1	0	2	0	0.1	0	1	0	2	0	0	0	0	0	0				X

	BEN Control						BEN Drift						BEN NoDrift						DFT	HYP	OVP	SED
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Berosus	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Coelostoma	0	0	0	0	0	0	0.1	0.2	0	1	0	6	0	0	0	0	0	0				
Hydrochara	0	0	0	0	0	0	0	0.2	0	1	0	4	0	0	0	0	0	0				
Laccobius	0.1	0.3	0	2	0	5	0.5	0.5	0	1	3	54	0.8	2.2	0	12	0	27	X	X		
Heteroptera	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Corixidae	0	0	0	0	0	0	0	0.2	0	1	0	4	0	0	0	0	0	0	X			
Micronectes	0	0	0	0	0	0	0	0.2	0	1	0	4	0	0.2	0	1	0	4				
Oligochaeta	0.7	1.5	0	7	0	30	0.6	0.5	0	1	3	57	4.8	12.8	0	66	1	62	X	X		
Trombidiformes	3.3	3.7	0	24	1	80	0.8	0.4	0	1	4	78	2.3	3.2	0	17	1	73		X		X
Ostracoda	0.2	0.4	0	2	0	13	0.5	0.5	0	1	3	48	0.9	1.7	0	7	0	31		X		X
Cyclopoida	1.2	2.3	0	12	0	45	0.6	0.5	0	1	4	65	2.6	4.5	0	21	1	58		X		X
Harpacticoida	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	1	0	2	X			
Cladocera	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0	X			
Collembola	0.1	0.4	0	2	0	12	0.1	0.3	0	1	0	9	0.2	0.5	0	2	0	13		X		
Crustacea																						
Gammarus	0	0	0	0	0	0	0	0	0	0	0	0	0	0.1	0	1	0	2				
Niphargus	1.9	5.2	0	37	0	40	0.1	0.3	0	1	1	13	0.9	3.1	0	20	0	21		X		
Isopoda	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0		X		

	BEN Control						BEN Drift						BEN NoDrift						DFT	HYP	OVP	SED
Taxa	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**	**Mean**	**SD**	**Min**	**Max**	**RA**	**FO**				
Others																						
Glossiphoniidae	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0				
Nematoda	0	0	0	0	0	0	0.1	0.3	0	1	1	9	0.2	0.4	0	2	0	15				
Gyraulus	0.1	0.2	0	1	0	5	0	0.2	0	1	0	4	0	0.1	0	1	0	2	X	X		
Hydrobiidae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				
Bythiospeum	1.1	8.0	0	62	0	5	0	0.1	0	1	0	2	0	0.1	0	1	0	2		X		
Physa	0	0	0	0	0	0	0	0.2	0	1	0	4	0	0	0	0	0	0	X		X	
Dugesia	0	0.1	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0				
Ephydridae	0	0	0	0	0	0	0	0.1	0	1	0	2	0	0	0	0	0	0				

CHAPTER 5:

GAMMARUS PULEX (CRUSTACEA: AMPHIPODA) AVOIDS INCREASING WATER TEMPERATURE AND INTRASPECIFIC COMPETITION THROUGH VERTICAL MIGRATION INTO THE HYPORHEIC ZONE: RESULTS FROM A MESOCOSM EXPERIMENT

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Chapter 5: *Gammarus pulex* avoids increasing water temperature and intraspecific competition through vertical migration into the hyporheic zone: results from a mesocosm experiment.

5.1 Abstract

The saturated sediments below and adjacent to the riverbed (i.e., hyporheic zone) can be a refuge for biota during disturbances, such as drying. Prior to drying, organisms are constrained by abiotic and biotic factors (e.g., water temperature, competition) and may respond through vertical migration into the hyporheic zone. However, it remains unclear when these factors become harsh enough to trigger this response. Furthermore, potential consequences of using the hyporheic zone, which is often food-limited, on the survival, ecosystem function and physiology of organisms are unknown. Using 36 mesocosms, the hypotheses that i) *Gammarus pulex* migrates into the hyporheic zone to avoid increasing surface water temperature and intraspecific competition and ii) migration would have negative consequences on the survival, leaf mass consumption and energy stores of organisms were tested. Three levels of temperature (15, 20, 25°C) and species density (low, medium, high) were manipulated in a factorial design over 15 days. Increased temperature to 25°C and a 3-fold increase in density both caused *G. pulex* to migrate into the hyporheic zone, but the interaction of these factors was not synergistic. Importantly, the survival, leaf consumption and glycogen content were reduced in high temperature and density treatments, indicating tradeoffs between tolerating harsh surface conditions and limitations in the hyporheic zone. Identifying that the hyporheic zone is used by invertebrates to avoid high water temperature and intraspecific competition is a key finding considering the global-scale increases in temperature and flow intermittence, yet its capacity to provide refuge is likely temporally limited.

Key words: stream drying, refuge, resistance, resilience, avoidance behavior, invertebrates

5.2 Introduction

The saturated interstitial areas beneath the riverbed and into the adjacent banks (i.e., hyporheic zone; White, 1993) have long been recognized for their potential to serve as a refuge for biota during disturbances (i.e., hyporheic refuge hypothesis; Palmer et al. 1992, Dole-Olivier et al. 1997, Stubbington 2012). They may also be a major source of colonization promoting the resilience of invertebrates (i.e., capacity to recover, Stanley 1994) following disturbances, such as flooding and drying (e.g., Holomuzki and Biggs 2007, Kawanishi et al. 2013, Vander Vorste et al. 2015 *in review*). Despite substantial empirical evidence showing that the physical characteristics of the hyporheic zone (e.g., % fine sediment, hydraulic conductivity, vertical hydraulic gradient) alter its potential to serve as

a refuge (e.g., Navel et al. 2010, Descloux et al. 2013, Mathers et al. 2014), the abiotic or biotic factors invertebrates respond to through vertical migration into the hyporheic zone remain speculative (Stubbington 2012). Among these factors, water temperature and biotic interactions are thought to be two of the most influential in triggering a behavioral response for stream invertebrates to enter the hyporheic zone (James et al. 2008, Wood et al. 2010, Stubbington et al. 2011).

Understanding the effects of increasing water temperature on the vertical migration of invertebrates into the hyporheic zone is critical in a context of global warming and water scarcity (Postel 2000, Datry et al. 2014, Jaeger et al. 2014). In many rivers, the increase in water temperature observed over the past 100 years ranges between 0.009–0.077 °C y^{-1} (Kaushal et al. 2010) and higher maximum temperatures (e.g., Mantua et al. 2010) are exceeding the physiological tolerance of aquatic organisms (Mouthon and Daufresne 2006, Wenger et al. 2011, Stewart et al. 2013a). For example, a 1.5°C increase in mean temperature combined with historically high summer temperatures (29.5°C max.) caused dramatic and long-lasting (>1 yr) declines in mollusk richness and diversity in the Saône River, France (Mouthon and Daufresne 2006). Moreover, increasing water scarcity issues and subsequent low flow, flow cessation and drying events in river systems (Postel 2000, Datry et al. 2014, Jaeger et al. 2014) exacerbate the general trend in water temperature increase. For example, during the initial contraction phase of drying streams, water temperature can reach above 25°C (e.g., Boulton 1989, Ludlam and Magoulick 2010). Insect larvae (e.g., Ephemeroptera, Plecoptera, Trichoptera), and crustaceans (e.g., Amphipoda, Isopoda) experience drastic increases in mortality between 21–25°C (Stewart et al. 2013a, Foucreau et al. 2014). To avoid thermal stress, invertebrates can migrate into the hyporheic zone, which is often several degrees cooler and remains buffered from highly variable surface temperatures (Constantz and Thomas 1997, Evans and Petts 1997). However, it is unknown at what temperatures invertebrates vertically migrate into the hyporheic zone, limiting our capacity to understand and predict the effects of global change on river community resilience. As climate change and water abstraction will continue to challenge river communities, quantifying the potential of the hyporheic zone to act as a refuge will be a key step towards predicting future responses of aquatic invertebrates (Keppel et al. 2015).

In addition to increased water temperature, vertical migration may occur when levels of biotic interactions increase, resulting notably from the contraction of aquatic habitat occurring during low flow, flow cessation and river drying (e.g., Power et al. 1985, Ludlam and Magoulick 2010). In particular, intraspecific competition for space and food can increase greatly following flow cessation (Lake 2003), as invertebrate densities reach up to 35 000 individuals (ind.) m^{-2} (e.g., Acuña et al. 2005). High density of *Chironomus riparius* (Diptera) resulted in up to 75% mortality of early instars, delayed development and increased migration to avoid competition (Silver et al. 2000). The hyporheic zone may provide refuge from intraspecific competition occurring on the surface (James et al. 2008, Stubbington et al. 2011); particularly because invertebrate densities in the hyporheic zone are

comparatively lower (Datry 2012, Capderrey et al. 2013). Furthermore, biotic interactions may increase (e.g., Scherr et al. 2010), decrease (e.g., Jiang and Morin 2004), or remain unaffected (e.g., Wooster et al. 2011) at high water temperatures, subsequently affecting vertical migration of surface-dwelling invertebrates into the hyporheic zone. Yet the constant interplay between water temperature and intraspecific competition in the natural environment render their effects difficult to disentangle using field surveys (Heino et al. 2015). Experimental approaches (e.g., mesocosms) can advance our understanding of the responses of invertebrates to multiple abiotic and biotic factors (Stewart et al. 2013b), and have been crucial to understanding vertical distribution of invertebrates at surface water and hyporheic zone interface (e.g., Nogaro et al. 2009, Navel et al. 2010, Vadher et al. 2015).

Despite the potential for invertebrates to seek refuge in the hyporheic zone to avoid the harmful effects of water temperature and/or biotic interactions occurring on the surface, their survival, ecosystem function and physiology may be jeopardized because food resources are often limited or of poor quality (Hervant et al. 1997, Burrell and Ledger 2003, Danger et al. 2012). For example, the surface invertebrate, *Gammarus fossarum*, subjected to starvation showed immediate hyperactivity and experienced mortality after 20 days (Hervant et al. 1997). Unless invertebrates can return to the surface to consume leaf litter (e.g., Elliott 2005, Navel et al. 2010), the decomposition of leaf litter on the surface will be considerably reduced when surface detritivores enter the hyporheic zone. Moreover, at the physiological level, invertebrate triglycerides and glycogen contents, two major energy stores involved in reproductive physiology and defense against environmental stress, may be considerably reduced within 1–2 weeks of the absence of food (Hervant et al. 1999). Therefore, use of a food-limited environment (the hyporheic zone) by invertebrates to avoid high temperatures and biotic interactions on the surface represents a tradeoff that may undermine the capacity of the hyporheic zone to provide refuge during disturbances.

In this study, we measured the effect of temperature and intraspecific competition on the vertical migration of the common stream shredding detritivore, *Gammarus pulex* (Crustacea: Amphipoda) into the hyporheic zone. We hypothesized that the hyporheic zone would be used as a refuge by this species to avoid high water temperature and intraspecific competition. We also hypothesized that migration into hyporheic zone would have negative effects on the survival, leaf consumption and energy stores of organisms. Based on these hypotheses, we predicted that: i) a higher proportion of organisms would migrate into the hyporheic zone as water temperature and species density increased, and ii) that the survival, leaf mass consumption rate and energy stores would decrease at the highest temperature and species densities. We also examined the potential interaction effect (synergistic, antagonistic, additive) of water temperature and intraspecific competition on the vertical migration of *G. pulex* into the hyporheic zone.

5.3 Methods

5.3.1 Study organism and collection site

Gammarus pulex is a widespread and common surface-dwelling shredder that is important in leaf litter degradation across European streams (MacNeil et al. 1997, Dangles and Malmqvist 2004, Piscart et al. 2011). All individuals were collected from a small stream near Dijon, France (47°24′13″N, 04°52′57″E), where species identity was previously confirmed through DNA analysis (Foucreau et al. 2013). During collection, sieves between 2.5–5.0 mm were used to select similar-sized individuals. Individuals were returned to a temperature-controlled (15 ± 2°C) room and allowed to acclimatize to laboratory temperature, water quality and food source for a 14-day period (Navel et al. 2010) before the start of the experiment. Water temperature was kept constant (15 ± 2°C) using a thermostatic water pump (TECO, Ravena, Italy) and oxygen concentrations were maintained near saturation with oxygen bubblers. During this time, individuals were fed alder leaves (*Alnus glutinosa*) collected in the autumn at a nearby river bank, air-dried and stored at room temperature.

5.3.2 Mesocosm description

Mesocosms (n = 36) were constructed from opaque PVC tubing (70 cm length × 25 cm diameter, 2 mm thickness) with a PVC end cap, forming a vertical column (Figure 5.1). To enumerate the individuals that migrated into the hyporheic zone, mesocosms were constructed in two parts, a 30-cm surface zone and a 40-cm hyporheic zone. These parts were joined during the experiment using PVC flanges (25 cm diameter) and allowed quick separation at the end of the experiment. Mesocosms were filled to a height of 50 cm with gravel substrate (10–14 mm) extracted from the Rhône River, France, leaving 10 cm of substrate in the surface zone (Figure 5.1). Dechlorinated tap water was continuously pumped from a 1000-L tank into the bottom of the mesocosms using two 24-channel peristaltic pumps at a rate of 1.25 L h^{-1}, creating a slightly positive vertical hydraulic gradient (i.e., upwelling movement of water) and constituting a complete renewal of mesocosm water volume in 24 h (Figure 5.1). Water drained through a hole (2 cm diameter), screened (0.5 cm mesh) to prevent invertebrates from escaping, located 5 cm below the top of each column. Surface water was aerated using an oxygen bubbler to keep dissolved oxygen (O_2) concentrations between 8.5–9.5 mg L^{-1}. A 12:12-h light:dark cycle was applied to the surface water zone using Grolux (35 W, 8500 K, Sylvania Inc., Noida, India) aquarium lights above mesocosms (Figure 5.1).

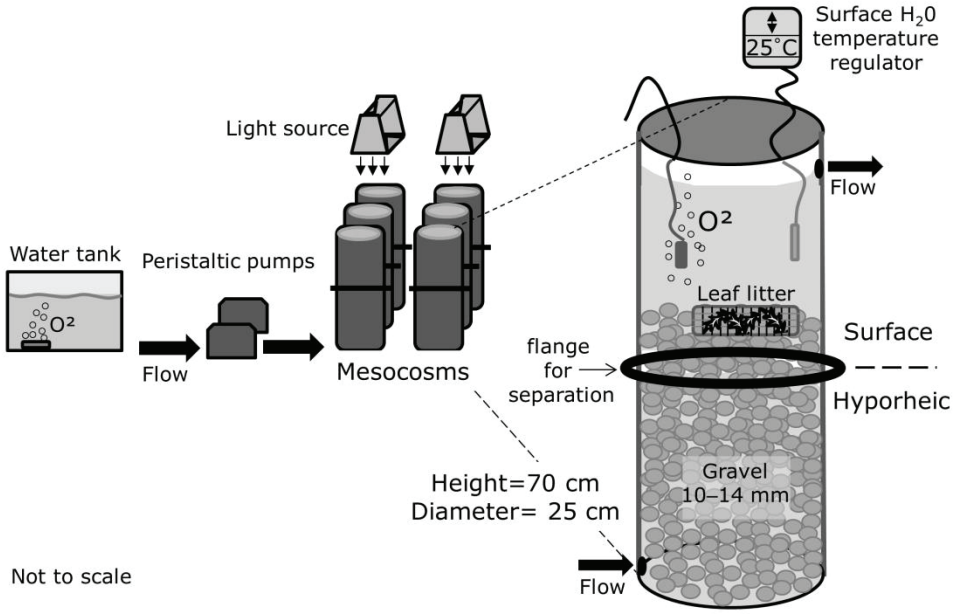

Figure 5.1 Experimental set-up of mesocosms (n = 36) used to test the effect of water temperature, species density and their interaction on the migration of *G. pulex* into the hyporheic zone.

5.3.3 Experimental design

Surface water temperature and species density were manipulated at 3 levels each in a factorial design over a 15-day period. Three treatments of temperature (15, 20 and 25°C) were tested (n= 12 mesocosms per temperature). To heat the surface water, a 10-m long heated cable (0.5 cm diameter) (Hydrokable, Hydor Inc. Sacramento, CA USA) was buried into the surface substrate and coiled around the inner wall of the mesocosms to the top of the surface zone. Surface water temperature was controlled using an electronic thermostat (± 0.1°C) (Hobby, Dohse Aquaristik GmbH & Co., Grafschaft, Germany). Surface and hyporheic water temperature was recorded hourly using iButton loggers (Maxim Integrated, San Jose, CA USA). For the unheated temperature treatment (15°C) (see below), an equally sized cable was similarly installed to account for the possible effect cables might have on vertical migration. Water temperature in the hyporheic zone was kept at 15.5 ± 0.5°C (mean ± SD) throughout the experiment, representing an approximate mean temperature reported from several rivers and providing a thermal refuge for organisms (Constantz and Thomas 1997, Evans and Petts 1997, Stubbington et al. 2011). For the first 24 hours of the experiment, water temperature was kept constant (15.2 ± 0.3°C) across all treatments. After this acclimatization period, temperatures were increased to the treatment level at a rate of 0.2°C h^{-1} for 20°C and 0.4°C h^{-1} for 25°C treatments over a 24-h period to avoid thermal shock of the organisms (Stewart et al. 2013a). Surface water temperature was then kept constant until the end of the experiment.

Three species density treatments, based on previous field surveys reporting *G. pulex* densities (Welton 1979, Elliott 2005), were tested (n= 12 mesocosms per density). A low density treatment of 40 ind. mesocosm^{-1}, corresponding to 815 ind. m^{-2}, was used to represent density treatments having little or no intraspecific competition. Density was increased 3-fold to 120 ind. mesocosm^{-1} (2444 ind. m^{-2}) to induce moderate levels of intraspecific competition (i.e., medium density). A high density treatment of 500 ind. mesocosm^{-1} (10 183 ind. m^{-2}) was used to induce high levels of intraspecific competition. For each treatment, individuals were counted by hand before being transferred into mesocosms using a small-hand net at the start of the experiment.

5.3.4 Proportion of individuals migrated into the hyporheic zone

The proportion of individuals that migrated into the hyporheic zone was quantified after 15 days by separating the surface and hyporheic zones of the mesocosms. For this, mesocosms were placed into a 60 × 80 × 40 cm plastic wash basin, with care taken to avoid agitation of the surface water that may cause organisms to redistribute vertically. The hyporheic zone was isolated from the surface zone by removing the stainless steel bolts that attached the two parts of the mesocosm and rapidly sliding the surface zone into the large basin, leaving the hyporheic zone of the mesocosm undisturbed. During this process, the water level in the columns was maintained until the moment of separation to avoid incidental migration of organisms into hyporheic zone. Substrate from each section was then sieved (500 µm) separately to recover all individuals from their respective zone.

5.3.5 Survival of organisms

Upon collection, all individuals were placed in white sorting trays and visually inspected for any movement. Individuals that did not survive the experiment were counted and separated from living individuals so they were not used for assays of triglycerides and glycogen (see below). Because *G. pulex* is known to feed on its dead conspecifics (MacNeil et al. 1997), individuals not found at the end of the experiment were presumed to be dead and consumed. Few individuals (<1%) appeared to be killed during the sampling effort (i.e. sieving); however, these individuals could not be reliably separated from individuals that did not survive the experimental treatments.

5.3.6 Measuring leaf consumption rate

In each mesocosm, 220 ± 10 mg of alder leaves with primary veins removed, dried at 60°C for 24 hours, were enclosed in 15 × 6-cm plastic mesh (10 mm diameter) bags. This mesh size allowed *G. pulex* to enter the bags freely and consume leaf litter. Leaf litter was pre-conditioned by immersing in river water for 10 days to allow for microbial colonization (mainly aquatic hyphomycetes) and

improve leaf palatability (Navel et al. 2010). After conditioning, one leaf litter bag was placed on the substrate surface of each mesocosm before the start of the experiment. Following the experiment, leaves were collected, dried at 60°C for 24 h and re-weighed. Leaf consumption rates (mg. ind.$^{-1}$ day^{-1}) were calculated as ((initial dry leaf mass)-(final dry leaf mass))/((# of individuals)*15 days). To correct final leaf mass consumption for leaching and microbial consumption not attributable to *G. pulex*, a temperature-specific correction factor was calculated based on the leaf mass loss in bags (n = 9) immersed in additional columns void of *G. pulex* for 15 days at each temperature level (Navel et al. 2010). Consumption rates were calculated based on the initial number and also the final number of individuals per mesocosm to account for survivorship and ensure that analyses of water temperature and species density effects on consumption rate were not biased by the method of calculating consumption rate.

5.3.7 Measuring triglycerides and glycogen contents

For triglycerides and glycogen assays, individuals collected at the end of the experiment were dried using an absorbent cloth, freeze-dried and weighed in groups of 3–4 individuals. Three replicate groups from each mesocosm were collected to establish mean triglycerides and glycogen contents. Groups were weighed (± 0.1 mg) and then ground into powder with a small mortar in pre-weighed glass tubes. Triglycerides and glycogen (µmol.g^{-1} dry mass) were extracted using standard enzymatic methods with prepared solutions (Sigma-Aldrich, Saint-Quentin Fallavier, France) described in further detail in Hervant et al. (1995) and Salin et al. (2010). Assays were made using an Aquamate spectrophotometer (Thermo Scientific Inc., Waltham, MA, USA) at 25°C.

5.3.8 Data analysis

Differences in the mean proportion of *G. pulex* that migrated into the hyporheic zone, percent survivorship, leaf mass consumption rate and triglycerides and glycogen contents between treatments were tested using a two-factor (two-way) analysis of variance (ANOVA). The design was a 3 (temperature levels: 15, 20, 25°C) × 3 (species density levels: low, medium, high) factorial design with interactions. Post hoc Tukey HSD multiple comparisons were used to compare mean levels within temperature and density treatment factors. Plotted residual variances and Levene's test were used to check for homogeneity of variance and normality and subsequently all percentages were arc($\sqrt{}$-x)-transformed and leaf mass consumption rates and triglycerides and glycogen content values were $\log_{10}(x)$-transformed to meet these assumptions. ANOVA and post hoc comparisons were made using *R* (version 3.1.1; R Project for Statistical Computing, Vienna, Austria).

5.4 Results

5.4.1 Effect of water temperature and species density on G. pulex migration into the hyporheic zone.

The proportion of individuals that migrated into the hyporheic zone tended to increase as water temperature and species density increased (ANOVA, temperature effect: $F_{2, 27} = 4.28$, $P = 0.024$, density effect: $F_{2, 27} = 11.354$, $P < 0.001$; Figure 5.2, Table 5.1). The proportion of organisms that migrated was higher in the 25°C treatments than at 15°C (Tukey HSD, $P = 0.030$; Figure 5.2), but not different than the proportion measured in the 20°C treatments. At high species density, the proportion of organisms that migrated was greater than in medium density (Tukey HSD, $P = 0.003$) and low density treatments (Tukey HSD, $P < 0.001$; Figure 5.2). The effect of water temperature on the proportion of individuals that migrated did not increase at high density (ANOVA, temperature × density effect: $F_{4, 27} = 1.65$, $P = 0.191$; Figure 5.2, Table 5.1).

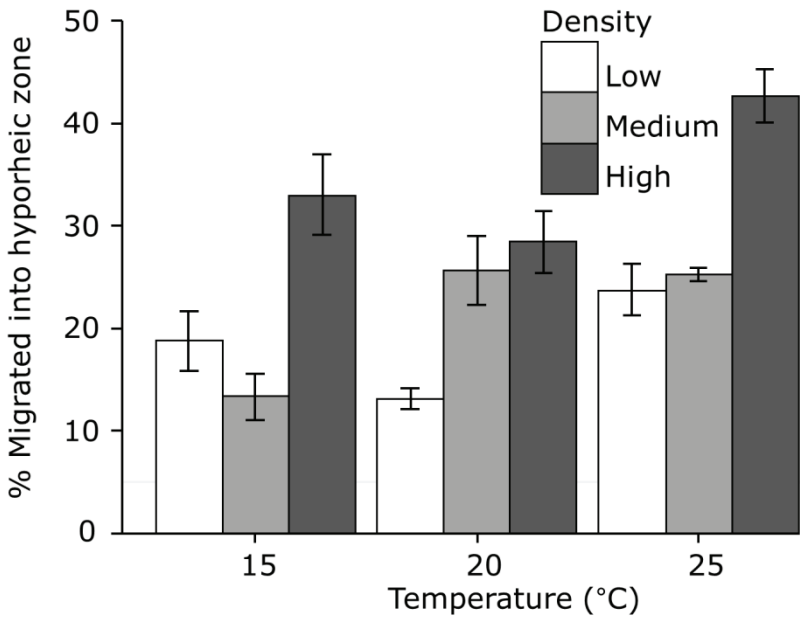

Figure 5.2 Mean (± SE) proportion (percent) of *G. pulex* that migrated into the hyporheic zone at different temperature and species density treatment conditions. Percent migrated into hyporheic zone is based on the initial species density.

Table 5.1 Mean (± SD) percent survivorship of *G. pulex* in different temperature and species density treatment conditions after the 15-day experiment.

Temperature	Species density	Mean	Min. – Max.
15°C	low	61 ± 8	55 – 73
	medium	62 ± 8	54 – 71
	high	67 ± 6	58 – 72
20°C	low	79 ± 5	73 – 85
	medium	67 ± 4	62 – 70
	high	63 ± 3	59 – 67
25°C	low	34 ± 12	23 – 48
	medium	35 ± 2	33 – 37
	high	48 ± 7	42 – 57

5.4.2 Effect of water temperature and species density on survival of G. pulex

The proportion of organisms that survived the experiment decreased as water temperature increased and there was an interaction effect of water temperature and species density (ANOVA, temperature × density effect: $F_{2, 27} = 5.64$, P = 0.002; Table 5.1, Table 5.2). The proportion of survival across low and medium densities was lowest at 25°C compared to survival measured at 15 and 20°C (Tukey HSD, P < 0.001 for all), whereas survival in the high density treatment at 25°C differed from survival in the high density treatment at 15°C (Tukey HSD, P = 0.02; Table 5.1, Table 5.2) but not the high density treatment at 20°C.

Table 5.2 Results from 2-way ANOVA testing the effect of temperature and species density and their interaction on dependent variables related to *G. pulex*. Percentages were arcsin(√-x)-transformed and leaf mass consumption rate, triglycerides and glycogen contents were log10(x)-transformed.

Dependent variable	Factor	d.f.	MSS	*F*	*P*
% Migrated	Temperature (T)	2	0.045	4.280	0.024
	Density (D)	2	0.119	11.354	<0.001
	T × D	4	0.017	1.650	0.191
% Survivorship	Temperature (T)	2	0.343	65.869	<0.001
	Density (D)	2	0.008	1.559	0.229
	T × D	4	0.029	5.640	0.002
Leaf mass consumption	Temperature (T)	2	1.975	38.091	<0.001
	Density (D)	2	1.087	15.120	<0.001
	T × D	4	1.734	15.931	<0.001
Triglycerides content	Temperature (T)	2	0.959	0.727	0.493
	Density (D)	2	0.940	0.459	0.637
	T × D	4	1.082	1.240	0.319
Glycogen content	Temperature (T)	2	2.869	2.461	0.105
	Density (D)	2	2.517	0.563	0.577
	T × D	4	3.902	4.013	0.012

5.4.3 Effect of water temperature and species density on the leaf mass consumption rate of G. pulex.

Leaf consumption rate of *G. pulex* based on the initial density was affected by water temperature, species density and their interaction (ANOVA, temperature × density effect: $F_{2, 26} = 15.93$, $P < 0.001$, Figure 5.3, Table 5.2). Consumption rate in the 20°C and 25°C treatments was lowest at medium and high species densities compared to low density (Tukey HSD, $P < 0.001$ for all) but at 15°C, different consumption rates were only detected between low and high density treatments (Tukey HSD, $P < 0.001$, Figure 5.3). Similarly, consumption rate based on the final density was also affected by the interaction of water temperature and species density (results shown in Appendix 5.1).

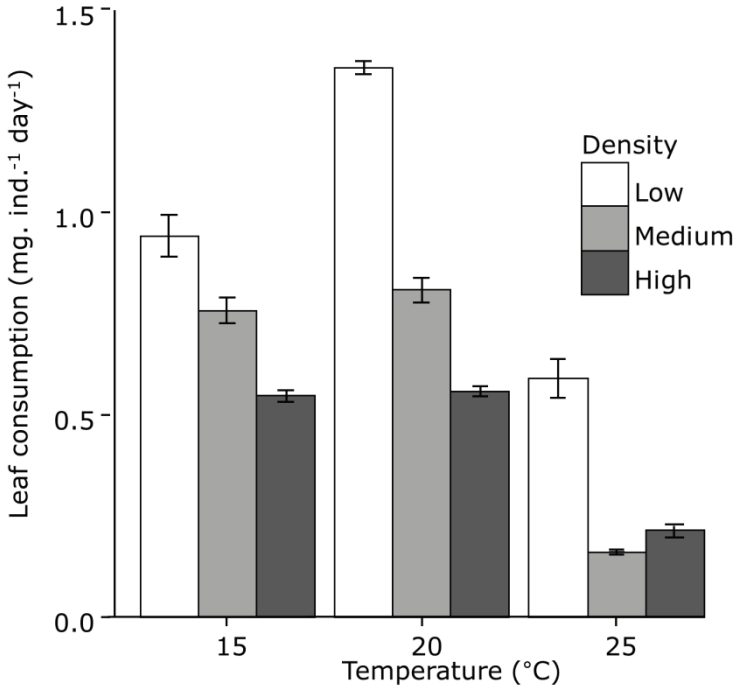

Figure 5.3 Mean (± SE) leaf mass consumption rate of *G. pulex* (mg. ind.$^{-1}$ day^{-1}) at different temperature and species density treatment conditions. Calculation based on initial species density.

5.4.4 Triglycerides and glycogen contents of organisms using the hyporheic zone

Mean triglycerides content did not differ among the levels of water temperature, species density nor by the interaction of these factors (Table 5.2). For mean glycogen content, the effect of water temperature was not consistent across different levels of species density (ANOVA, temperature × density effect: $F_{4, 26} = 4.013$, $P = 0.012$; Figure 5.4, Table 5.2). Glycogen content at high and medium densities was lower than glycogen content at low density in the 20°C treatment (Tukey HSD, $P = 0.004$ for both), whereas there was no difference in glycogen content among low, medium and high densities at 15°C.

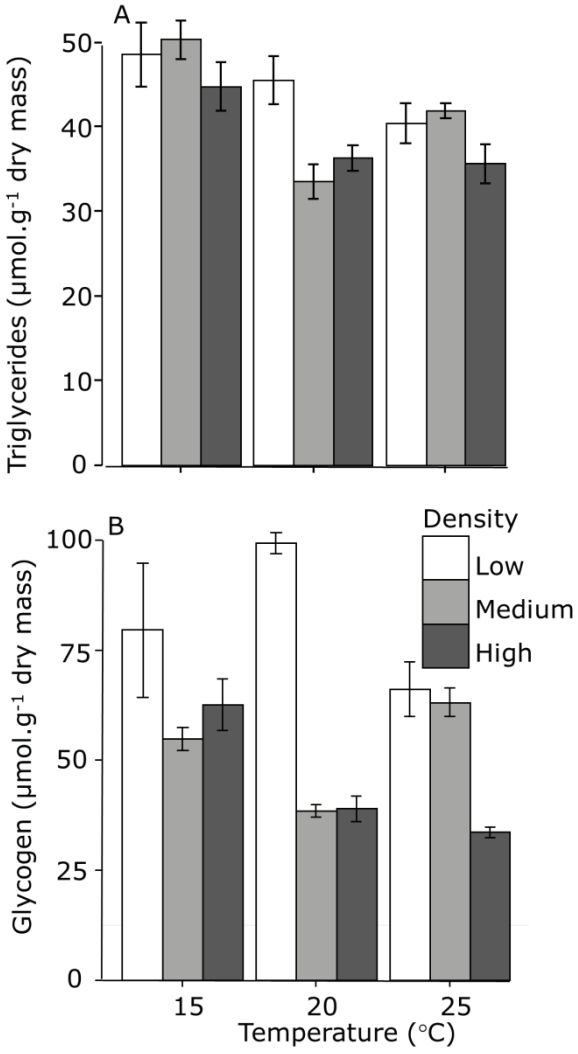

Figure 5.4 Mean (± 1 S.E) individual triglycerides (µmol.g^{-1} dry mass) (a) and glycogen content (µmol.g^{-1} dry mass) (b) of *G. pulex* at different temperature and species density treatment conditions.

5.5 Discussion

5.5.1 Influence of water temperature and species density on vertical migration into the hyporheic zone

In agreement with our first prediction, both increasing water temperature and intraspecific competition led to the migration of *G. pulex* into the hyporheic zone. These findings imply hyporheic refuge use is an active process in which invertebrates use abiotic and biotic cues to avoid the harsh surface conditions that coincide with low flow, flow cessation and drying events. Water temperature above 20°C caused a higher proportion of individuals to use the hyporheic zone. This threshold closely matches the temperature (24°C) when *G. pulex* survival becomes drastically reduced in short-term (10 days) enclosed exposures (Foucreau et al. 2014). For intraspecific competition, a 3-fold increase in

species density (2400 ind. m^{-2}) led to a higher proportion of individuals using the hyporheic zone. In previous behavior experiments with *G. pseudolimnaeus*, Williams and Moore (1985) found a 3.5-fold increase in species density increased the number of individuals entering the substrate. Our results mirror those from two previous studies investigating hyporheic refuge use by invertebrates (Wood et al. 2010, Stubbington et al. 2011). Wood et al. (2010) reported peak invertebrate densities in the hyporheic zone when surface water temperature around 20°C was reached in the Little Stour River, UK; whereas Stubbington et al. (2011) found the highest proportion of *G. pulex* in the hyporheic zone, relative to the surface, during a low-flow period in the River Lathkill, UK, when the highest density (2449 ind. m^{-2}) occurred. Our mesocosm approach complemented these field surveys by disentangling the individual and combined effects of water temperature and intraspecific competition and identifying thresholds that will help predict the responses of invertebrates to low flow, flow cessation and river drying.

Biotic interactions (e.g., competition, predator-prey relationships) can intensify with increasing water temperature (Burnside et al. 2014), leading to unexpected responses of species in aquatic systems (Ormerod et al. 2010). However, in this study, the effect of intraspecific competition of *G. pulex* on the proportion of individuals that migrated into the hyporheic zone did not appear to increase when temperatures were increased up to 25°C (i.e., additive response). The absence of a synergistic response may be attributed to the behavior of *G. pulex* at temperatures above its thermal tolerance. At temperatures above its thermal tolerance, activity rates and metabolism can decrease sharply (e.g., Foucreau et al. 2014), which may have led to a decrease in conspecific encounters, hence, reducing competition (Wooster et al. 2011). Therefore, biotic interactions may increase with water temperature until the point when thermal tolerance is exceeded, which is between 21–25°C for most aquatic invertebrates (Stewart et al. 2013a, Foucreau et al. 2014), and individuals reduce their activity in a final attempt to conserve energy and avoid death.

Our results, along with those from previous field studies (e.g., Wood et al. 2010, Stubbington et al. 2011), bolster evidence that the hyporheic zone is an important refuge for riverine invertebrates avoiding increased water temperatures and biotic interactions. These results have important implications considering the projected global-scale increases in water temperatures and flow intermittence (Postel 2000, van Vliet et al. 2013, Datry et al. 2014). In particular, water stressed regions, such as the American Southwest, may see a 27% increase in the median number of days of flow cessation and a 15-day increase drying event duration by mid-century, respectively (Jaeger et al. 2014). Changes in flow regime will be coupled with average increases in global mean and maximum river water temperatures up to 1.6°C which will, in turn, increase evaporation and drying rates (van Vliet et al. 2013). If organisms can survive temporarily in the hyporheic zone and return to the surface when conditions become favorable, it is likely that, in at least some systems (e.g., alluvial rivers), the

hyporheic zone can be the primary source of resilience for invertebrate communities (Vander Vorste et al. *in review*).

Future experiments may aim to test the effects of different abiotic and biotic factors that could also influence invertebrate use of the hyporheic zone. For example, dissolved oxygen saturation in receding river pools can be as low as 6% (e.g., Boulton 1989) and when coupled with high water temperatures will likely increase the negative effects on invertebrates and consequently, migration of invertebrates into the hyporheic zone would be strongly increased. Depth of the water table below the riverbed may also be an important factor limiting the colonization and return to surface for invertebrates (Vander Vorste et al. *in review*). Furthermore, interspecific competition and predation often increase simultaneously in drying rivers (Lake 2003) and may trigger migration of invertebrates into the hyporheic zone (Stubbington 2012). Invertebrate migration into the hyporheic zone may decrease predation risk from fish and large invertebrates (e.g., Fairchild and Holomuzki 2005), and reduce top-down effects in river pools (Boersma et al. 2014). Finally, the direction of vertical hydraulic gradient (i.e., upwelling, downwelling) is likely an overriding physical force controlling vertical migration of invertebrates (Olsen and Townsend 2003, Capderrey et al. 2013, Mathers et al. 2014). In this study, the fact that mesocosms had slightly upwelling water strengthens evidence that *G. pulex* actively sought refuge in the hyporheic zone, rather than passively following the direction of water movement. In general, higher abundances of surface invertebrate are found in downwelling reaches (e.g., Dole-Olivier et al. 1997, Olsen and Townsend 2003, Capderrey et al. 2013), presumably aided by the downward movement of water. Therefore, it is expected that *G. pulex* would show a greater response to enter the hyporheic zone in downwelling river reaches. Although, vertical migration may have been related to the rheophilic nature of *G. pulex* or its ability to detect cooler temperatures in the upwelling water. Future mesocosm experiments can facilitate exploration into how these various factors will influence hyporheic zone use by invertebrates in drying rivers.

5.5.2 Decreased survival, leaf litter consumption and energy stores

In agreement with our second prediction, use of the hyporheic zone as a refuge had negative effects on survival, leaf litter consumption and energy stores of *G. pulex*. In this study, the hyporheic zone in mesocosms mimicked conditions in the natural streams, where the availability of food resources are generally limited and/or of poor quality (Burrell and Ledger 2003, Danger et al. 2012). Consequently, the low rates of survivorship (39 ± 7%; mean ± SD) and decreased glycogen content of *G. pulex* in high temperature treatments suggested that starvation could have become a factor during this 15-day experiment. Previous studies have shown surface invertebrates appear highly susceptible to mortality during periods of starvation (Hervant et al. 1997, 1999), especially compared to hypogean taxa. Therefore, food resources may be an important limiting factor that influences invertebrate survival in the hyporheic zone.

As a consequence of migration into the hyporheic zone, the processing of leaf litter by invertebrates on the riverbed may be substantially reduced during periods of low flow, flow cessation, and stream drying (Corti et al. 2011, Datry et al. 2011, Dehedin et al. 2013). In this study, a 63 ± 7% reduction in leaf litter consumption per individual between 20 and 25°C suggested that *G. pulex* did not return to the surface to feed after entering the hyporheic zone. This result contrasts with recent studies suggesting that leaf litter decomposition will increase with rising water temperatures due to enhanced microbial decomposition and invertebrate activity rates (e.g., Ferreira and Canhoto 2015, Mas-Martí et al. 2015). However, we argue that decomposition rates will be reduced when rising temperatures are coupled with contraction and drying of aquatic habitats and subsequent competition for resources due to the behavioral response of shredding invertebrates to enter the hyporheic zone. Implications of these findings are important considering *G. pulex* were responsible for an estimated 13% of leaf litter consumption in a wooded stream (Mathews 1967) and several other invertebrate shredders (e.g., Leuctridae, Leptoceridae) are known to use the hyporheic zone during disturbances (Stubbington 2012). An important next step will be to test if invertebrates are able to track diel water temperature changes, returning to the surface at night when surface temperatures are cooler to feed and how this may compensate for energy loss during the day.

River invertebrates face a tradeoff between tolerating harsh surface conditions versus avoiding them by entering the hyporheic zone, a strategy which may not be suitable for long-term survival. On one hand, lower water temperature, fewer conspecific interactions and the lack of large predators may entice invertebrates to migrate into the hyporheic zone during periods of low flow, flow cessation and drying. On the other hand, once in the hyporheic zone, food limitation, low oxygen concentration (Findlay 1995) and colmation (Descloux et al. 2013), especially in rivers impacted by agricultural land use, will reduce the capacity of the hyporheic zone to provide refuge. Furthermore, competitive and predatory interactions with hypogean taxa (e.g., Schmid and Schmid-Arraya 1997) are likely to occur, although quantifiable evidence must be explored further. These interactions may have negative or positive effects on the resilience of surface invertebrates, depending on the outcome of these interactions. Therefore, the potential cascading effects of hyporheic zone refuge use by invertebrates remains an important research gap that could be addressed through mesocosm experiments.

5.5.3 Conclusion

There is a strong need to understand the influence of factors, such as water temperature and biotic interactions, that coincide with low flow, flow cessation and drying on river communities, especially considering global change will continue exacerbate their negative effects on river systems (Postel 2000, Datry et al. 2014, Jaeger et al. 2014). In many regions, once perennial rivers are now becoming intermittent (Datry et al. 2014), therefore future studies could explore how trait variability (Violle et

al. 2012) and differences in physiological tolerance (Stoks et al. 2014) among populations from formally perennial and naturally intermittent rivers influence the response to increased temperature and biotic interactions. Although rare in freshwater ecology, the use of common garden experiments (i.e., simultaneously subjecting different populations to the same stressor) have revealed strong inter-population differences in temperature tolerance within aquatic species (e.g., Foucreau et al. 2014). Therefore, such approaches could be developed to explore the responses of populations from perennial and intermittent rivers to other environmental factors associated with river contraction and drying. These experiments will in turn help refine the predictions of population and community responses to global climate change and increased water abstraction.

5.6 Acknowledgements

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Appendix 5.1 Results from 2-way ANOVA testing the effect of temperature and species density and their interaction on leaf mass consumption of *G. pulex*. Leaf mass consumption rate was log10(x)-transformed. Leaf mass consumption based on final number of individuals to account for survivorship though it was not possible to determine when organisms died during the experiment.

Dependent variable	Factor	d.f.	MSS	*F*	*P*
Leaf mass consumption	Temperature (T)	2	1.104	0.409	0.669
	Density (D)	2	1.920	9.943	<0.001
	T × D	4	1.649	3.390	0.024

CHAPTER 6:

INCREASED DEPTH TO THE WATER TABLE DURING RIVER DRYING DECREASES THE RESILIENCE OF *GAMMARUS PULEX* AND ALTERS ECOSYSTEM FUNCTION

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Chapter 6: Increased depth to the water table during river drying decreases the resilience of *Gammarus pulex* and alters ecosystem function

6.1 Abstract

River drying has drastic immediate effects on benthic invertebrates but high resilience reduces its long-term effects on biodiversity and ecosystem functions (e.g. leaf litter decomposition). The hyporheic zone (saturated interstitial sediments) can be a refuge for invertebrates during drying and a primary source of colonists that supports resilience following re-inundation. However, little is known about factors, such as the depth to the water table below the riverbed, which could limit this capacity. We explored how depth to the water table (control, –5 cm, –30 cm, completely dry) during a one-week drying event affected the survival and return to the surface (%RTS) of *Gammarus pulex* (Crustacea: Amphipoda) in laboratory mesocosms. We measured leaf litter decomposition and glycogen energy stores to examine effects on ecosystem function and energetic costs related to organisms burrowing deeper into the hyporheic zone. Two populations, collected from intermittent and perennial rivers, were used to evaluate inter-population variability in the response to drying. Survival and %RTS were reduced by ≤ 39% and 52%, respectively, in the –30 cm and dry treatments and this had cascading effects on decomposition (≤ 46% reduction). Differences between populations in %RTS were high across all treatments but did not generally affect survival and decomposition. Our results suggest that increases in depth to the water table during river drying, which often result from longer drying duration and water abstraction, could reduce invertebrate resilience and ecosystem function by diminishing the role of the hyporheic zone as a source of colonization.

Keywords: hyporheic zone, recovery, intermittent rivers, alluvial rivers, leaf litter decomposition, mesocosms, climate change, water abstraction

6.2 Introduction

In many regions, intermittent rivers (i.e. those that cease to flow and experience periodic loss of surface water) comprise the majority of river networks (Datry *et al.* 2014). Moreover, global climate change and anthropogenic pressures (e.g. water abstraction) are increasing the frequency and duration

of drying events and can even lead to drying of perennial rivers (Gleick 2003, Döll and Schmied 2012, Jaeger *et al.* 2014). River drying is an important driver of aquatic invertebrates that can lead to the immediate loss of species richness and altered composition (Bogan and Lytle 2011, Datry *et al.* 2014) and subsequent decreases in ecosystem functions such as leaf litter decomposition (Langhans and Tockner 2006, Datry *et al.* 2011). However, resilience (i.e. capacity to return to pre-disturbance levels) of aquatic biota following flow resumption can be high, reducing long-term effects on biodiversity and ecosystem functions (Fritz and Dodds 2004, Leigh *et al.*, 2015, Vander Vorste *et al.* 2015). For example, invertebrate taxonomic richness and functional diversity in intermittent alluvial rivers typically recovers less than one month after flow resumption (Fowler 2004,Vander Vorste *et al.* 2015). Yet, in other cases, the resilience of communities can be low (e.g. Wood and Armitage 2004) and this can have cascading effects onto ecosystem function by altering the rate of leaf litter decomposition (LLD; Datry *et al.* 2011, Corti *et al.* 2011). The rate of LLD in the intermittent Albarine River (France) following drying decreased due, in part, to the limited recovery of detritivore communities (Datry et al. 2011). Understanding the processes that promote community resilience has become a major research focus of freshwater ecology because it can lead directly to the management and restoration of river systems that are resilient to future environmental change (Lake *et al.* 2007, Palmer *et al.* 2008).

The vertical migration of benthic invertebrates into and from the hyporheic zone (i.e. the saturated sediments below and adjacent to the riverbed; White 1993) can promote community resilience in rivers (Williams and Hynes 1976, Dole-Olivier 2011, Vander Vorste *et al.* 2015). During drying events, invertebrates avoid high temperatures, intraspecific competition (e.g. Vander Vorste *et al.*, In review) and desiccation (e.g. Vadher *et al.* 2015) by migrating into the underlying hyporheic zone. When flow resumes, the hyporheic zone can then be the primary source of community resilience (e.g. Kawanishi *et al.* 2013, Vander Vorste *et al.* 2015). However, the potential of the hyporheic zone to be a source of resilience varies with its accessibility to invertebrates. For instance, fine sediments can completely prevent invertebrate migration by clogging interstitial pore space in the hyporheic zone (Navel *et al.* 2010, Descloux *et al.* 2013, Vadher *et al.* 2015). Consequently, leaf litter decomposition is reduced when shredding invertebrates are unable to migrate into or return from the hyporheic zone, as shown in mesocosm experiments (Navel *et al.* 2010, Vander Vorste *et al.*, In review). Identifying the factors that limit vertical migration of invertebrates has become a major focus in rivers because of their potential to reduce the mitigating effects of the hyporheic zone following river drying (Dole-Olivier 2011, Stubbington 2012).

The depth to the water table (i.e. the thickness of the vadose zone between the streambed surface and the saturated hyporheic zone) is an important factor that can determine whether the hyporheic zone is used as a refuge during drying events. The water table depth generally remains shallow in river reaches with upwelling conditions (gaining reaches); whereas, depth can gradually increase during

drying in reaches with downwelling conditions (losing reaches) due to transmission loss of surface water into the substrate (Boulton 2003, Datry *et al.* 2007, Larned *et al.* 2011). When rivers are perched above the regional aquifer, the hyporheic zone may become dry to depths of 1–14 m soon after water has disappeared from the surface (e.g. Datry 2012). In this case, organisms will be forced to burrow/crawl further into the hyporheic zone, which will likely increase energetic cost (Shepard *et al.* 2013) and risk of becoming stranded in dry substrate (Stumpp and Hose 2013). It is still unclear how water table depth influences the subsequent return of invertebrates to the surface (i.e. their resilience) and if there are cascading effects on key ecosystem functions, such as leaf litter decomposition, which hinge on invertebrate resilience in intermittent rivers. As more perennial rivers become intermittent due to climate change and surface and groundwater abstraction (Gleick 2003, Döll and Schmied 2012, Döll *et al.*, 2012, Jaeger *et al.* 2014), understanding how changes in water table depth influence communities and ecosystem function is necessary to predict the effects of global change on river communities.

The shift of perennial to intermittent flow regimes in many regions has also sparked the need to consider the population-level variability in the response of aquatic organisms to disturbance. Populations of the same species can vary in their response to environmental conditions because of local adaptation (Kawecki and Ebert 2004, Chapuis and Ferdy 2012). Local adaptation is a process in which traits evolve differently among populations (*i.e.* divergent selection), despite the potential for inter-population dispersal and gene flow, and will improve the fitness of organisms in a local population to its local environmental conditions (Kwecki and Ebert 2004). Therefore, it is expected that a population should outperform (e.g. higher survival) another population under conditions for which it has become adapted to because differences in physiological tolerance and/or trait attributes (Kawecki and Ebert 2004). For example, populations of adult *Galba truncatulata*, a freshwater snail, collected from intermittent rivers were more tolerant to desiccation than populations from perennial rivers (Chapuis and Ferdy 2012). These studies suggest that a similar response of populations originating from intermittent and perennial rivers to drying cannot be assumed.

In this study, we explored how the depth to the water table influenced the resilience of benthic invertebrate populations and LLD following a one-week drying event. We tested this on *G. pulex*, a common and important shredding invertebrate that inhabits both intermittent and perennial European rivers. We predicted that increasing water table depth would reduce the resilience of *G. pulex* populations because organisms would be more likely to become stranded in the hyporheic zone and face a higher risk of desiccation associated with having to burrow further into the substrate. In turn, we predicted that altered population resilience would have cascading effects on ecosystem function by altering leaf litter decomposition. Lastly, we predicted that glycogen energy stores of *G. pulex* would be reduced when water table depth increased as a result of the increased energetic costs of migrating further into and from the hyporheic zone. To evaluate the potential influence of local adaptation on

population-level responses to drying and use the hyporheic zone, we tested two populations of *G. pulex*, one collected from an intermittent river in the Mediterranean region of France and one from a perennial river located in temperate France.

6.3 Methods

6.3.1 Study organism and collection sites

Gammarus pulex was used to test our predictions about the effects of water table depth on resilience, ecosystem function and energy stores because it is a common species across European streams and plays an important role on LLD, a key ecosystem function in rivers (Mathews 1967, Dangles and Malmqvist 2004, Handa *et al.* 2014). Two populations of *G. pulex* were collected within one-week of each other (April 2015) from small tributaries in the Rhône River Valley, France. Population 1 (Pop1) was collected from the intermittent Seguissous River near Bouquet, France (04°16'20.4"E, 44°10'06.1"N). The Seguissous is a 3rd order river (width = 3 m, depth = 0.5 m; average at sampling location) with coarse gravel substrate that dried during the summer months of the sampling year (re-visited August 2015), like most rivers of this size in the Mediterranean region of France (Snelder *et al.* 2013). Population 2 (Pop2) was collected from a tributary to the Suzon River near Dijon, France (04°52′57″E, 47°24′13″N). This small 1st order tributary (width = 1.5 m, depth = 0.3 m: average at sampling location) also has coarse gravel substrate but flows perennially, as confirmed by previous visits (February–July, 2014; Vander Vorste *et al.*, In review).

We confirmed the species identity of each population through morphology and molecular analysis. A subsample of individuals (n = 100) from each population were identified using a dissecting microscope and a regional taxonomic key (Piscart and Bollache 2012). Following the experiment, molecular analysis was performed on 10 individuals from Pop1 and 7 individuals from Pop2 (previously been confirmed from this sampling location by Foucreau *et al.* (2013). For this analysis, DNA (cytochrome c oxidase subunit I (COI)) was extracted (Walsh *et al.* 1991, Lagrue *et al.* 2014), amplified (LCO1490 and HCO2198; Folmer *et al.* 1994) and sequenced (Sanger *et al.* 1977) to allow comparisons of genetic distances (Lefébure *et al.* 2006) to be made with known haplotypes (Lagrue *et al.* 2014). These comparisons confirmed the morphological identification of *G. pulex*, except for a single individual from Pop2 that corresponded to *G. fossarum.* Of the individuals identified as *G. pulex,* corresponding to Group A in Lagrue *et al.* (2014), there was ≤ 12% genetic distance between the two populations, which is below the threshold (16%) identified by Lefébure *et al.* (2006) for distinct crustacean species. Nevertheless, genetic divergence between populations indicated the presence of two clades and therefore a potential of different responses to water level treatments due to local adaption to environmental conditions.

Before the experiment, populations were kept in separate aquariums (40 x 22 x 25 cm) in a temperature-controlled (15 ± 2°C) room and allowed to acclimatize to laboratory temperature, water quality and food source for a 7–14 day period (Navel *et al.* 2010). Dechlorinated tap water was kept at a constant temperature (15 ± 2°C) using a thermostatic water pump (TECO, Ravena, Italy) and oxygen concentrations were maintained near saturation. Alder leaves (*Alnus glutinosa*), immersed in river water for 10 days to allow for microbial colonization (mainly aquatic hyphomycetes) and improve leaf palatability (Graça *et al.* 1993), were provided as a food source.

6.3.2 Mesocosm description

Thirty-two mesocosms were constructed from opaque PVC tubing (70 cm length × 25 cm diameter, 2 mm thickness) with a PVC end cap, forming a vertical column (Vander Vorste *et al,.* In review). Each mesocosm had two sections, a 30-cm surface zone and a 40-cm hyporheic zone, to allow separation and enumeration of individuals that returned to the surface following drying events. These two sections were fixed during the experiment using PVC flanges (25 cm diameter) but allowed quick separation at the end of the experiment. Coarse gravel (10–14 mm), extracted from the Rhône River, France, was washed and dried to provide a realistic substrate that, based on porosity, would not limit the vertical migration of *G. pulex* (Navel *et al.* 2010). Water was continuously pumped from a 1000-L tank into the bottom of the mesocosms using two 24-channel peristaltic pumps at a rate of 1.6 L h^{-1} (1 renewal of water volume/24 h), creating a slightly positive vertical hydraulic gradient (i.e., upwelling movement of water). Water exited mesocosms through a hole (2 cm diameter) located 5 cm below the top of each column that was screened (0.5 cm mesh) to prevent invertebrates from escaping. Surface water was aerated using an oxygen bubbler to keep dissolved oxygen (O_2) concentrations between 8.5–9.5 mg L^{-1}. A 12:12-h light:dark cycle was applied to the surface water zone using Grolux (35 W, 8500 K, Sylvania Inc., Noida, India) aquarium lights above mesocosms. More details on the mesocosms are provided in Vander Vorste *et al.* (in review) and a short video explaining construction of mesocosm is available at http://dx.doi.org/10.6084/m9.figshare.1544573.

6.3.3 Experimental design

To explore the influence of water table depth on the resilience of *G. pulex* following drying events, a factorial experimental design was used to test the effects of 4 water level treatments across the two populations of *G. pulex* (4 replicate mesocosms per water level × population treatment combination). Water level treatments were control (i.e. no drying), –5 cm and –30 cm below the sediment surface and dry (Figure 6.1). At the start of the experiment, 120 individuals of *G. pulex* (7–10 mm body length) were placed in each mesocosm using a small hand-net and left to acclimatize for 24 hours. Mesocosms were then dried for 7 days by removing a plug from the pre-installed drain at the

respective location on each column to allow water to slowly seep out of the mesocosm over a 48-h period. In the –5 and –30 cm water table depth treatments, water was continuously pumped into the hyporheic zone to avoid stagnation after water table treatment depths were reached. In the completely dry treatment, water was completely absent from the mesocosms, however, substrate remained moist during the drying event. To estimate sediment moisture, which could influence the short-term tolerance of *G. pulex* to desiccation (Stubbington and Datry 2013), two additional columns were used in which the completely dry treatment was applied. Moisture content was measured by weighing sediments collected following one-week of drying from the upper 10 cm and the bottom 10 cm of mesocosms before and after oven drying for 24 hours at 60°C. In the dry treatment, moisture content in the upper 10 cm of sediments was 0.8 ± 0.1% (Mean ± S.D.) and 1.8 ± 0.1% in the bottom 10 cm of sediments during the final day of drying.

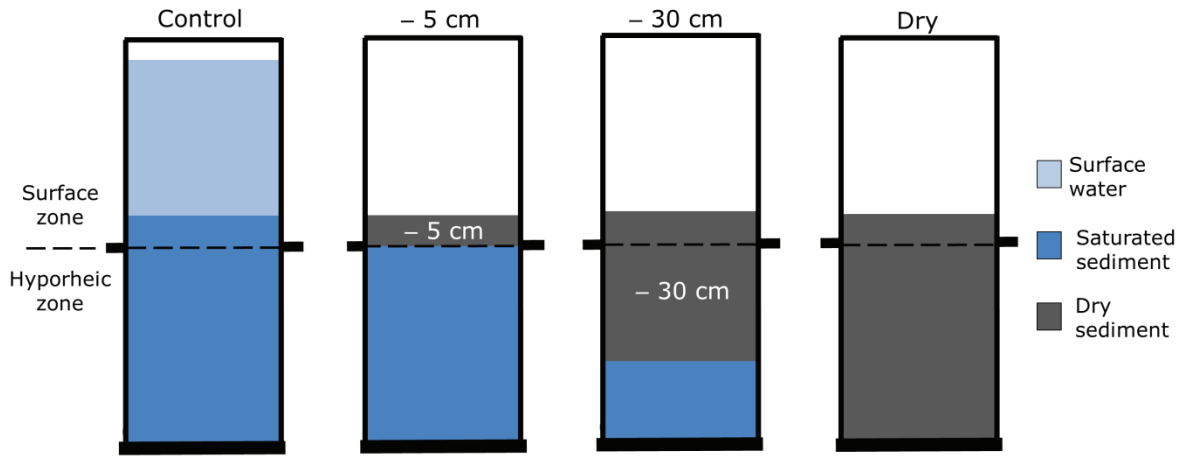

Figure 6.1 Experimental design used in mesocosms (n = 32), showing the 4 water table depth treatments (Control, –5 cm, –30 cm and dry) with their respective levels of surface water, saturated sediments and dry sediments

After drying events, drain plugs were reinstalled and columns were allowed to fill with water to the pre-drying level within 6 h. After 7 days of re-inundation to allow invertebrates to return from the hyporheic zone to the surface (Vander Vorste *et al.* 2015), individuals of *G. pulex* were collected from the surface and hyporheic zones of the mesocosms.

Individuals were collected at the end of the experiment by placing mesocosms into a 60 × 80 × 40 cm basin, with care taken to avoid agitation of the surface water that may cause organisms to redistribute vertically. The hyporheic zone was then separated from the surface zone by removing the stainless steel bolts that attached the two sections of the mesocosm and rapidly sliding the surface zone into the large basin, leaving the hyporheic zone of the mesocosm undisturbed. During this process, the water level in the columns was maintained until sections were separated to avoid incidental migration of

organisms into hyporheic zone. Finally, the substrate from each section was then sieved (500 µm) to recover all individuals from their respective zone to calculate the proportion that returned to the surface (details in Vander Vorste *et al.*, In review, http://dx.doi.org/10.6084/m9.figshare.1544573).

6.3.4 Survival of individuals

Upon collection, all individuals were placed in sorting trays and visually inspected for any movement to assess the proportion of individuals that survived the experiment. Individuals that did not survive were counted and separated from living individuals so they were not used for glycogen assays (see below). Because *G. pulex* is known to feed on its dead conspecifics (MacNeil *et al.* 1997), individuals not found at the end of the experiment were presumed to be dead and consumed.

6.3.5 Leaf litter decomposition

To assess how limited population resilience could have cascading effects by altering ecosystem process rates, 4.05 ± 0.1 g of alder leaves, with primary veins removed and dried at 60°C for 24 hours, were enclosed in 15 × 6 cm plastic mesh (10 mm diameter) bags. Mesh bags allowed *G. pulex* to enter freely and decompose leaf litter. Leaf litter was pre-conditioned by immersion in river water for 10 days to allow for microbial colonization (mainly aquatic hyphomycetes) and improve leaf palatability (Navel *et al.* 2010). After conditioning, one leaf litter bag was placed on the substrate surface of each mesocosm just before re-inundation began. Following the experiment, leaves were collected, dried at 60°C for 24 h and re-weighed. Leaf litter decomposition (g) was calculated as the difference between initial and final leaf weight.

6.3.6 Measuring glycogen contents

To assess the effect of water table depth on energetic costs, all surviving individuals from each mesocosm were combined, freeze-dried, weighed (± 0.1 mg) and ground into powder with a small mortar in pre-weighed glass tubes (n = 32). Glycogen (µmol.g^{-1} dry mass) was extracted using standard enzymatic methods with prepared solutions (Sigma-Aldrich, Saint-Quentin Fallavier, France) described in further detail in Hervant *et al.* (1995) and Salin *et al.* (2010). Assays were made using an Aquamate spectrophotometer (Thermo Scientific Inc., Waltham, MA, USA) at 25°C (Vander Vorste *et al.*, In review).

6.3.7 Data analysis

The proportion of individuals that returned to the surface (% RTS) was calculated based on the number of individuals that survived the experiment. Differences in the % survival, % RTS, LLD and glycogen contents were tested using a two-factor (two-way) analysis of variance (ANOVA). The design was a 4 (water level: control, – 5 cm, – 30 cm and dry) × 2 populations (Pop1 and Pop2) factorial design with interactions. Post hoc Tukey's HSD multiple comparisons were used to compare mean levels within drying and population treatment factors. Residual variances and Levene's test were used to check for homogeneity of variance and normality and subsequently all percentages were arc(√-x)-transformed and leaf mass consumption rates and glycogen content values were $\log_{10}(x)$-transformed to meet these assumptions. Leaf litter decomposition was further tested using linear regression for the relationship between decomposition and the number of surviving individuals. All analyses were made using R (version 3.1.1; R Project for Statistical Computing, Vienna, Austria).

6.4 Results

6.4.1 Survival of *Gammarus pulex*

Survival of *G. pulex* differed among the water table depth treatments and populations and there was a significant water level × population interaction effect indicating differences in survival between populations were not consistent across water table depth treatments (Figure 6.2a, Table 6.1). In both populations, there was no difference between the –5 cm and control treatment (Tukey's test, $P > 0.05$; Figure 6.2a). Reductions of 29–39% in survival, compared to the control treatment, occurred when water level was lowered to –30 cm (Tukey's tests, Pop1, $P = 0.009$, Pop2, $P < 0.001$) and in the completely dry treatment (Tukey's tests, Pop1, $P < 0.001$, Pop2, $P = 0.005$), respectively (Figure 6.2a, Table 6.1). The comparison of the two populations showed that survival in Pop2 was two-fold higher than in Pop1 in the dry treatment (Tukey's test, $P < 0.001$) whereas survival did not differ between populations in the other table depth treatments (Tukey's tests, $P > 0.05$; Figure 6.2a, Table 6.1).

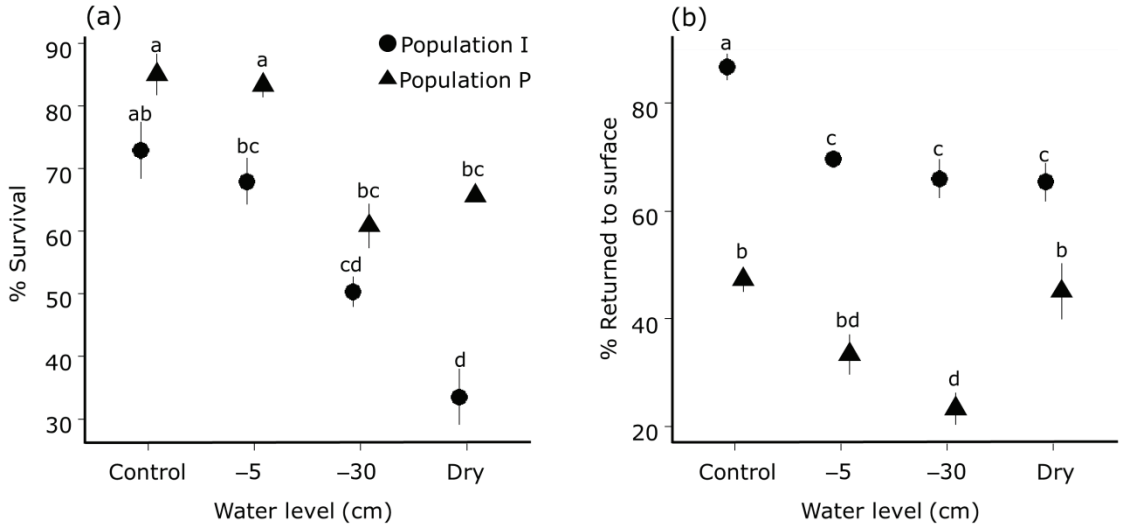

Figure 6.2 Mean ± S.E. of % survival (a), % returned to the surface (%RTS) (b) following a 1 week of drying and 1 week of re-inundation. Treatments with the same letters are not significantly different (post hoc Tukey's test, $p > 0.05$).

Table 6.1 Results from two-way ANOVA testing the effects of water table depth treatment (control, –5 cm, –30 cm and dry), population (Population 1 and Population 2) and the treatment × population interaction on the survival (%), proportion of individuals returned to the surface (%) of *Gammarus pulex* following one-week of drying and one-week of re-inundation.

	Water table depth				Population				Water table depth × Population			
Dependent Variable	*df*	SS	*F*	*P*	*df*	*SS*	*F*	*P*	*df*	*SS*	*F*	*P*
% Survival	3	0.415	23.659	< 0.001	1	0.047	8.085	0.009	3	0.053	3.026	0.050
% Returned to surface	3	0.176	11.274	< 0.001	1	0.396	76.119	< 0.001	3	0.074	4.744	0.010

6.4.2 Proportion of individuals returned to the surface

Of the individuals that survived the experiment, the % RTS differed among drying treatments and populations and there was significant water level × population interaction effect, indicating differences between populations in the % returned to the surface were not consistent across water table depth treatments (Figure 6.2b, Table 6.1). In Pop1, reductions of 20–24% in the % RTS occurred in –5 cm, –30 cm and completely dry treatments compared to the control treatment (Tukey's tests, $P = 0.007$, $P = 0.003$, $P < 0.001$, respectively), but these reductions were not greatest in the –30 cm and completely dry treatments (Tukey's tests, $P > 0.05$, Figure 6.2b, Table 6.1). In Pop2, the % RTS was not reduced in the –5 cm treatment nor the completely dry treatment, compared to the control (Tukey's tests, $P > 0.05$; Figure 6.2b, Table 6.1). There was, however, a reduction of 52% in the –30cm treatment compared to the control treatment (Tukey's test, $P < 0.001$). Pop2 had 1.5–3-fold decrease in the % RTS compared to Pop1 in all water table depth treatments (Tukey's tests, $P < 0.01$, for all).

6.4.3 Leaf litter decomposition

Water table depth treatments had significantly different effects on leaf litter decomposition but there were no differences in leaf litter decomposition between populations and no water level × population interaction, indicating that the feeding activities of the two populations on surface were similarly affected by water level treatments (Figure 6.3a, Table 6.2). Leaf litter decomposition was not reduced, compared to the control, in the –5 cm water table depth treatment (Tukey's test, $P > 0.05$), but there was a 38–46% decrease in leaf mass consumed in the –30 cm treatment (Tukey's test, $P = 0.001$) and the completely dry treatment (Tukey's test, $P < 0.001$; Figure 6.3a, Table 6.2). Leaf litter decomposition was strongly and positively correlated with the % survival of *G. pulex* in the experiment ($R^2 = 0.38$, $P < 0.001$, $n = 31$), whereas no correlation was observed between LLD and % RTS ($R^2 = –0.01$, $P = 0.442$, $n = 31$; Figure 6.3b).

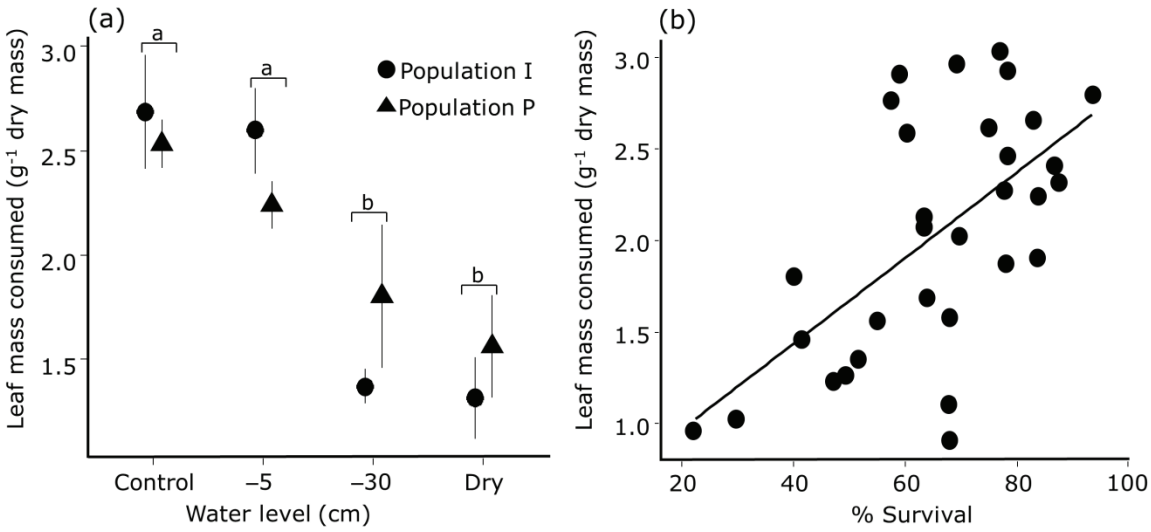

Figure 6.3 Mean ± S.E. of leaf mass consumed following 1 week of re-inundation (a). Linear correlation between leaf litter decomposition and the % survival of both populations of *G. pulex* (R^2 = 0.38, $P < 0.001$) (b). Treatments with the same letters are not significantly different (post hoc Tukey's test, $p > 0.05$).

Table 6.2 Results from two-way ANOVA testing the effects of water table depth treatment (control, –5 cm, –30 cm and dry), population (Population 1 and Population 2) and the treatment × population interaction on the leaf mass consumed (g), glycogen content of *Gammarus pulex* following one-week of drying and one-week of re-inundation.

	Water table depth				Population				Water table depth × Population			
Dependent Variable	*df*	SS	*F*	*P*	*df*	*SS*	*F*	*P*	*df*	*SS*	*F*	*P*
Leaf mass consumed	3	2.383	13.214	< 0.001	1	0.020	0.326	0.573	3	0.175	0.969	0.424
Glycogen content	3	0.415	15.528	< 0.001	1	0.001	0.137	0.715	3	0.063	2.368	0.097

6.4.4 Glycogen content of *Gammarus pulex*

Of the individuals that survived the experiment, there were differences in mean glycogen content among drying treatments but not between populations and no water level × population interaction effect, indicating that energy stores of the two populations were similarly affected by water level treatments (Figure 6.4, Table 6.2). Mean glycogen content was not reduced in the –5 and –30 cm treatments compared to the control (Tukey's tests, $P > 0.05$, Figure 6.4). In the dry treatment, there was a 25% reduction in mean glycogen content compared to the control treatment (Tukey's test, $P < 0.001$, Figure 6.4).

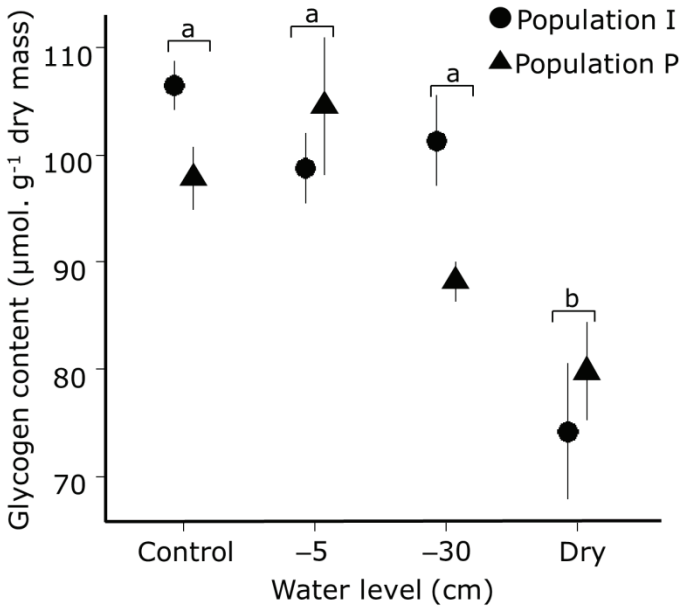

Figure 6.4 Mean ± S.E. of glycogen content measured in Gammarus pulex following 1 week of re-inundation. Treatment groups (brackets) with the same letters are not significantly different (post hoc Tukey's test, $p > 0.05$).

6.5 Discussion

6.5.1 Effect of water table depth during drying events on resilience

In agreement with our first prediction, the resilience of *G. pulex* to drying was negatively affected by increasing water table depth. There were large reductions in survival (up to 39%) and the proportion on individuals that returned to the surface (% RTS; up to 52%) for treatments with water table of 30 cm below the sediment surface, indicating that water table depth is an important consideration when studying invertebrate community resilience in intermittent rivers. The likely mechanism behind the decrease in resilience is that *G. pulex*, a species adapted to swimming (Elliott 2002), was forced to

burrow or crawl into the substrate to reach saturated conditions. The hyporheic zone presents a maze-like corridor of interstices in which organisms face a high risk of becoming stranded in dry sediments during drying events (Stumpp and Hose 2013). Although it has been previously shown that small substrate size reduced benthic invertebrate migration into the hyporheic zone (Navel *et al.* 2010, Descloux *et al.* 2013, Vadher *et al.* 2015), we showed that invertebrates can be also filtered in coarse gravels (10–14 mm) during drying events, when the water table depth decreases to ≥ 30 cm below the substrate surface. This offers a possible explanation for why benthic invertebrates are rarely collected at depths > 100 cm during drying events (Clinton *et al.* 1996, Boulton and Stanley 1995). However, few studies have performed invertebrate sampling at these depths in the hyporheic zone. Our results expand on previous studies by showing that the filtering effect of the hyporheic zone can directly affect the resilience of populations.

6.5.2 Cascading effects on ecosystem function and energy stores

Leaf litter decomposition was reduced by up to 46% when the water table depth was lowered to –30 cm and in the dry treatments due to mortality and a lower proportion of individuals returning to the surface. This demonstrates that a reduction in invertebrate resilience can have cascading effects on ecosystem functions. Our results have important implications in intermittent rivers considering *Gammarus* spp. contributes greatly to LLD , a primary ecosystem function recognized in rivers (Mathews 1967, Dangles and Malmqvist 2004, Handa *et al.* 2014). For example, *Gammarus* spp. comprised 83 ± 13% of detritivore abundance in a temperate river (Handa *et al.* 2014). Mathews (1967) estimated that *G. pulex* was responsible for 13% of LLD in a wooded stream in England. Loss of *Gammarus* spp. from the detritivore community during drying events could mean that other detritivores may face less competition for food resources and could compensate for leaf litter decomposition (i.e. insurance hypothesis; Yachi and Loreau 1999). However, few other detritivores are as efficient at leaf litter decomposition (Piscart *et al.* 2011) or reach comparable abundances to *Gammarus* spp. (Dangles and Malmqvist 2004). This makes their resilience to drying crucial to ecosystem function in many European rivers. Cascading effects of drying on LLD may continue downstream because LLD constitutes a major source of fine particulate organic matter (FPOM) to downstream communities (e.g. filter feeders) (Vannote *et al.* 1980, Cuffney *et al.* 1990). For example, reduced richness and abundance of detritivores caused by insecticide disturbance resulted in a 33% decrease in the annual FPOM transported downstream of a headwater stream (Cuffney *et al.* 1990). At broader scales, a reduction in LLD due to drying (e.g. Langhans and Tockner 2006, Datry *et al.* 2011) could have a significant influence on biogeochemical cycles considering intermittent rivers comprise an estimated 50% of the global river network (Datry *et al.* 2014). However, broad-scale effects of flow intermittence on carbon and nutrient cycles are only beginning to be estimated (von Schiller *et al.* 2014).

For surviving *G. pulex*, glycogen energy stores consumed during the drying event because of energy costs associated with migration and lack of leaf litter in the hyporheic zone were re-stored within one-week of re-inundation, except in the completely dry treatment where glycogen content remained 25% lower than the control treatment. This confirms a previous study indicating th*at Gammarus* spp. can be resilient to short-term starvation (28 days for *G. fossarum*, Hervant *et al.* 1999) but shows that short-term desiccation in the dry sediments posed a greater stress on organisms (i.e. more energy consumption) and energy stores could not be fully restored following re-inundation. For benthic invertebrates, short-term starvation in the hyporheic zone is likely because leaf litter conditioning by aquatic hyphomycetes is greatly reduced compared on the surface (Cornut *et al.* 2014). Furthermore, buried leaf litter is inherently less accessible to benthic detritivores (Piscart *et al.* 2011). Indeed, when measured in the field, leaf litter decomposition is markedly lower in the hyporheic zone compared to on the surface (Cornut *et al.* 2010, Piscart *et al.* 2011). Therefore, it is unlikely that increased leaf litter decomposition in the hyporheic zone during drying events by benthic invertebrates will compensate for loss of this function on the surface. Future experiments that quantify the duration that different invertebrate taxa can survive in the hyporheic zone could test how longer drying events (e.g. 1–3 mos) will affect the resilience of invertebrates.

6.5.3 Population-level variability in hyporheic zone use

Populations of *G. pulex* collected from intermittent and perennial rivers did not differ in their survival or leaf litter decomposition following re-inundation in the –5 and –30 cm water table depth treatments, despite contrasting use of the hyporheic zone. These results contrast with previous studies that have shown differences in physiological tolerance (Foucreau *et al.* 2014) and desiccation resistance (Chapuis and Ferdy 2012) that favored the survival of populations under conditions that they were most adapted. Therefore, we would have expected the intermittent river population to be more resilient to drying than the perennial population based on the results from these previous studies. One potential explanation for the lack of population-level differences in resilience is that the drying events generated during this experiment did not include the harsh abiotic and biotic factors that typically are associated with river drying. For example, factors such as temperature and biotic interactions can serve as environmental cues that initiate invertebrate migration (Vander Vorste *et al.*, In review), and without these cues the population from the intermittent stream may have behaved differently than during a natural drying event.

Strong differences in hyporheic use between populations, which could not be associated with water table depth, may have been responsible for the 2x greater survival in the perennial river population compared to the intermittent river population. This result is surprising because it contradicts previous evidence that intermittent river populations have higher desiccation tolerance than those from

perennial rivers (Chapuis and Ferdy 2012). Instead, it suggests that a high proportion of individuals (~50%) inhabiting the hyporheic zone may have buffered the negative effects of an increasing water table depth by lowering the risk of individuals from becoming stranded near the sediment surface during the drying event. Individuals stranded near the surface by increasing water table depth were potentially less tolerant to desiccation because of a lower moisture content compared to deeper substrates (0.8% vs 1.8%; Stubbington and Datry 2013, Poznańska *et al.* 2013). Differences in hyporheic zone use between populations could not have been caused by size, which was controlled for during the experiment, but may be related to other abiotic (e.g. direction of surface-groundwater exchange) or biotic (e.g. presence of predators) conditions that normally present in their respective habitats. Future studies could explore environmental factors that induce such strong differences in habitat use between populations. Common garden experiments offer a useful approach to test hypothesis about which environmental factors have acted as selective pressures or drivers of population-level variability (Kawecki and Ebert 2004, Chapuis and Ferdy 2012). Because this study did not exhaustively test for population-level differences that could indicate local adaptation to river drying, we suggest that future studies could explore these differences using several replicate populations per hydrological condition (intermittent *vs* perennial). To this end, molecular analysis must be used to confidently distinguish responses attributable to drying from those caused by genetic differences among populations (Colson-Proch *et al.* 2009).

6.5.4 Spatio-temporal limitations of the hyporheic zone as a source of colonization

Water table depth during drying events in alluvial rivers depends primarily on the regional hydrogeological setting which controls the level of the regional aquifer below the riverbed and the duration of drying events (Boulton 2003, Datry *et al.* 2007, Larned *et al.* 2011). Near geological knickpoints (i.e. sharp change in valley width or channel slope; Stanford and Ward 1993; Capderrey *et al.* 2013), water generally remains flowing perennially but as alluvial rivers become unconfined and water is lost into the subsurface (losing reaches), reaches often dry for periods of several weeks to months during the summer (e.g. Doering *et al.* 2007, Vander Vorste *et al.* 2015). These losing reaches can comprise between 7–78% of the river length (e.g. Konrad 2006) and be as long as 29 km (e.g. Doering *et al.* 2007). During drying events, the water table in losing reaches can lower at rates of 5 cm per week (e.g. Clinton *et al.* 1996) to 9 cm per day (Stella *et al.* 2010), depending on the porosity of the substrate. Based on our results, in losing reaches that are perched above the alluvial aquifer regional aquifer level, water table depth may exceed the depths that invertebrates are able to colonize within a few weeks to months after surface water dries. Therefore, the contribution of the hyporheic zone as a source of colonization following drying events will be lowest in perched losing reaches that experience drying events (Dole-Olivier 2011, Datry 2012). The relationship between water table depth and invertebrate resilience should be tested across multiple taxa that use the hyporheic zone (e.g.

Chironomidae, Leptophlebiidae, Leuctridae) during drying events and at greater depths than those used in this study to develop more accurate predictions on the spatio-temporal limitations of the hyporheic zone during drying events

6.5.5 Implications for river management and climate change

The hyporheic zone can be a primary source of colonization following flow resumption in intermittent rivers (Williams 1977, Fowler 2002, Vander Vorste *et al.* 2015). However, its contribution to community resilience is closely linked to the hydromorphological characteristics that control the vertical migration of invertebrates (Navel *et al.* 2010, Descloux *et al.* 2013, Vadher *et al.* 2015). In this study, we have shown that increasing the depth to the water table can reduces community resilience to river drying. These results have important implications considering that climate change and increased water abstraction are predicted to increase the extent and duration of drying events at a global scale (Gleick 2003, Döll and Schmied 2012, Jaeger *et al.* 2014). Our results suggest that even small changes (< 1 m) in water table depth could reduce resilience and have cascading effects on ecosystem function. As climate change and water abstraction are poised to decrease community resilience by diminishing the role of the hyporheic zone as a source of colonization, it is important to also consider the cascading effects of drying on ecosystem function which can be closely linked to community resilience in intermittent rivers.

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CHAPTER 7:

SYNTHESIS AND PERSPECTIVES

Chapter 7: Synthesis and perspectives

Ecologists are faced with the daunting task of determining the processes that determine community assembly in a world experiencing unprecedented rates of global climate change (Mouquet *et al.* 2015). Community assembly is influenced by disturbances (Myers *et al.* 2015), which are now occurring with higher frequency and intensity than previously recorded (IPCC 2014). One such disturbance, drying, is a widespread phenomenon in many regions of the world, affecting more than 50% of the global river network (Datry *et al.* 2014). Despite this prevalence, our ecological understanding of intermittent rivers has lagged behind that of other aquatic ecosystems and this has hindered their protection and management (Acuña *et al.* 2014, Datry *et al.* 2014, Leigh *et al.* 2015). Drying is widely presumed to shape the richness, abundance and composition of aquatic communities (Williams 2006, Bonada *et al.* 2007, Datry *et al.* 2014). Yet relatively few studies have investigated the effects of drying on communities in naturally harsh environments, which may be less affected because they are dominated by species that are highly resilient to disturbance. Furthermore, little is known about which sources of colonization are most important for resilience of communities facing drying (Stanley et al. 1994, Fritz and Dodds 2004, Bogan *et al.* 2014). Together, these knowledge gaps make it difficult to identify processes that drive community assembly (deterministic or stochastic) and focus management efforts which will increase resilience of communities and the ecosystem functions they provide to future climate change.

In this thesis, my objective was to explore the community resilience in alluvial rivers by quantifying their resilience to drying, identifying the primary source of colonists contributing to this resilience (*i.e.* the hyporheic zone). Furthermore, I tested different evironmental factors that influence the use of the hyporheic zone by invertebrates. Through field observations, manipulative experiments and laboratory mesocosms, I found that (i) aquatic invertebrate communities are highly resilient to drying in alluvial rivers, (ii) the hyporheic zone is a primary source of community resilience, (iii) temperature and interspecific competition can initiate vertical migration into the hyporheic zone and (iv) increases in the depth to the water table reduce community resilience and alter ecosystem function. Below, I synthesize these key findings in broader context of freshwater ecology and river management. Finally, I provide future research perspectives which could advance the our understanding of processes that promote community resilience and lead directly to the improved management and restoration of river systems.

7.1 Alluvial rivers are highly disturbed but have high community resilience to drying

In the 8 alluvial rivers I studied, community resilience to drying events was higher than in other previously studied but less-disturbed systems (Chapter 3), supporting the idea that communities in highly disturbed systems can be less affected by disparate disturbances than to those in more

environmentally stable systems (Vinebrooke *et al.* 2004, Côté and Darling 2010). This idea is based on niche theory (Whittaker *et al.* 1973) in which local communities are comprised of species that have been filtered by their abiotic and biotic environment (Chase and Leibold 2003, Winemiller *et al.* 2015). In braided alluvial reaches, the combination of drying, flooding and channel instability creates a harsh abiotic environment that subsequently filters the number of species that are able to persist (Tockner *et al.* 2009). By comparison, headwater and meandering reaches of alluvial rivers with less extreme flow variability and greater channel stability support a more diverse species pool (Ward 1998, Finn *et al.* 2011). My study of braided alluvial rivers supports the theory that deterministic effects related to a harsh disturbance regime strongly influence species composition, increasing the proportion of resistant and/or resilient taxa and thereby increase community resilience.

My finding of high resilience in naturally highly disturbed communities help to inform the long-standing diversity-stability debate in ecology (MacArthur 1955, McCann 2000, Loreau and de Mazancourt 2013). Some ecologists argue that more diverse communities are more stable (*i.e.* return quickly to an equilibrium after a small perturbation away from equilibrium; McCann 2000) when faced with disturbances (MacArthur 1955, Ives and Hughes 2002, Loreau and de Mazancourt 2013). Potential mechanisms for a positive diversity-stability relationship include asynchrony in the responses of species to environmental fluctuations (because more species means more diverse responses), differences in the speed of response between species to disturbance and decreases in competition during unfavorable environmental conditions (Loreau and de Mazancourt 2013). In essence, a diverse community is more likely to contain species that are resilient to disturbances than a less diverse community; an idea known as the insurance hypothesis (Yachi and Loreau 1999).

Although there is evidence of positive diversity-stability relationships (Silver *et al.* 1996, Yachi and Loreau 1999, Côté and Darling 2010), a case can also be made for the existence of negative diversity-stability relationships in ecology. Disturbance regimes filter a broad species pool into one that only includes taxa with traits that confer resistance or resilience to the disturbances encountered. There is much evidence of this in aquatic communities; *e.g.* nestedness patterns along disturbance gradients indicate that as environmental conditions become harsher, local communities become increasingly dominated by a core group of taxa (found in all local communities within a region) that recover quickly after disturbances (Therriault and Kolasa 2001, Datry *et al.* 2014, Brendonck *et al.* 2015). My data from braided alluvial rivers provides further evidence of negative diversity-stability relationships in aquatic communities: local communities were dominated by 8−15 species with traits associated with resistance and/or resilience to drying. Further empirical support for a negative biodiversity-stability relationship comes from terrestrial (Cole *et al.* 2014) and marine ecosystems (Côté and Darling 2010, Neubauer *et al.* 2013). Together, this evidence forms an alternative view of the diversity-stability relationship whereby environmental harshness and associated species traits influence the resilience of communities and ecosystem functions (Silver *et al.* 1996, Côté and Darling 2010, Baskett *et al.* 2014).

Strengthening the support for high community resilience in harsh ecosystems, there is growing evidence of co-tolerance (Vinebrooke *et al.* 2004, Flöder 2012). Aquatic ecosystems are becoming increasingly affected by multiple disturbances, both natural and anthropogenic, and these disturbances may have synergistic or antagonistic effects on aquatic communities (Folt *et al.* 1999, Piggott *et al.* 2015). Synergistic effects (*i.e.* their combined effect is larger than predicted from the size of the response to each disturbance alone; Folt *et al.* 1999) can occur if tolerance of the community to one disturbance does not confer tolerance, or leaves a community more vulnerable, to another disturbance (*i.e.* negative co-tolerance; Vinebrooke *et al.* 2004). Whereas, antagonistic effects occur when communities that are tolerant to one disturbance type are also inherently tolerant to the second type of disturbance (Vinebrooke *et al.* 2004). My data indicate that many of the taxonomic traits that promote resistance and/or resilience to floods could also confer resistance and/or resilience to drying in alluvial rivers (Table 7.1).Therefore, consideration of the current and historical disturbance regime, which influences the importance of niche filtering and co-tolerance, is needed to accurately predict the effects of drying on aquatic communities and ecosystem functions.

Table 7.1 Invertebrate traits that may promote the resistance and/or resilience to flooding and drying. Rationale for traits was collected from previous literature (Lytle and Poff 2004, Vieira *et al.* 2004, Lepori and Hjerdt 2006, Bonada *et al.* 2007, Statzner and Beche 2010).

Trait	Rationale for co-tolerance
Small body size	Increased ability to use the HZ as a refuge during drying and floods; faster development to reach terrestrial adult stage
Strong swimming ability	Enables fast recolonization of previously dry or flooded channels from refuges
Resistance forms (eggs, statoblasts, cocoons, cells against desiccation and diapause or dormancy)	Capacity to resist desiccation during drying and less sensitive to harsh physicochemical conditions during floods
Ovoviviparity	Immediate hatching of eggs reduces egg mortality in harsh conditions associated with drying and floods.
Asynchronous egg hatching	Increases likelihood of survival to unpredictable drying and floods
Asexual reproduction	Enables reproduction without mates when abundance is low after drying and floods
Aerial respiration	Allows organisms to remain in dry channels or escape onto riparian areas to avoid floods
Short life span	Minimize time spent in drying or flood-prone habitats

The concept of co-tolerance suggests that current conceptual models that predict the relationship between drying and species richness or community composition (*e.g.* Bonada *et al.* 2007, Bogan *et al.* 2014, Datry *et al.* 2014) could be improved by including other factors that influence environmental harshness. For example, Fritz and Dodds (2005) found that a harshness index that included characteristics of both flooding and drying events was better at predicting invertebrate richness in intermittent prairie streams than one including only drying characteristics. Furthermore, Ward and Stanford (1995) predicted that harshness, mostly driven by low channel stability, in braided reaches of alluvial rivers will lower diversity relative to than in headwater and meandering reaches. Therefore, I propose a new conceptual model that predicts the resilience of communities to drying along the multi-disturbance gradient of environmental harshness typically present in alluvial river corridors (Figure 7.1). This model will help ecologists and managers predict where drying will be most influential on aquatic communities of alluvial rivers subject to multiple natural and human-induced disturbances and ecosystem functions.

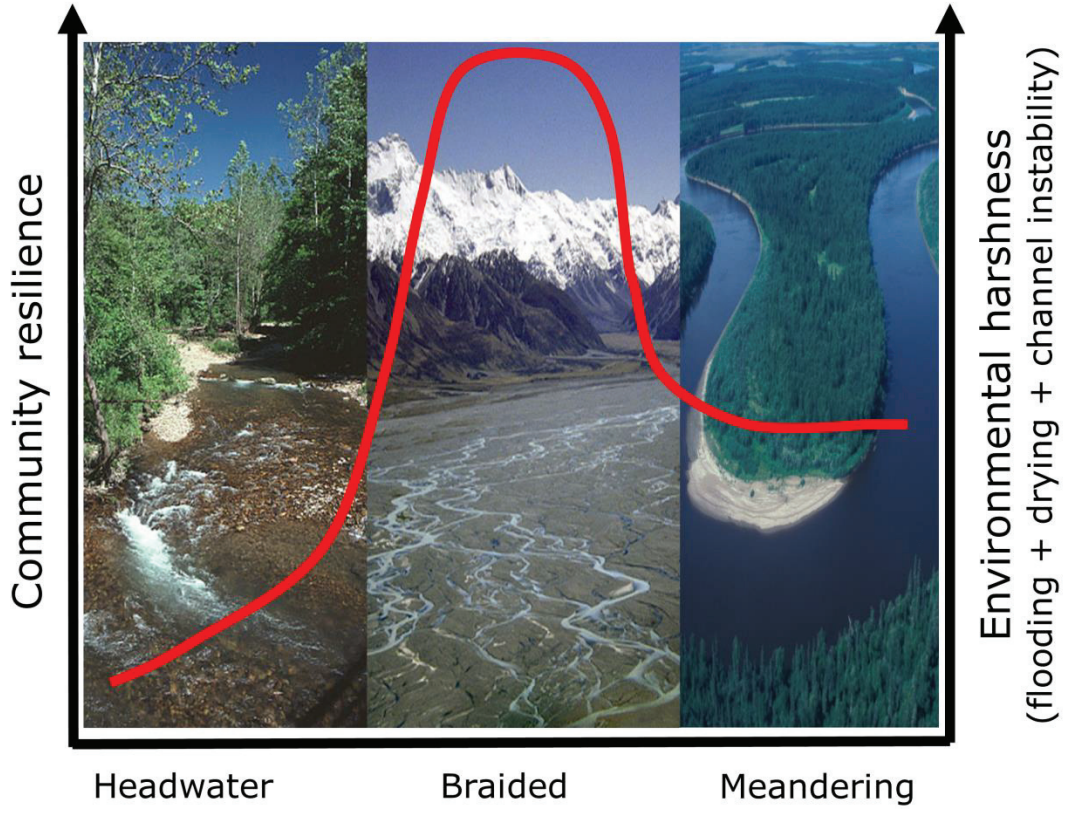

Figure 7.1 Conceptual model illustrating the proposed relationship between community resilience and environmental harshness in an idealized alluvial river. Environmental harshness (floods, drying and channel instability) peaks in braided reaches, whereas harshness is generally lower in headwater and meandering reaches. Therefore, the effect of environmental filtering and likelihood of species co-tolerance should be highest in braided reaches and communities should be dominated by species that are highly resilient to multiple distubrbances (Photographs credits, from left to right, are to Gary P. Flemming, Euan Mearns and US Fish and Wildlife Service).

7.1.1 Management implications

My study shows that increases in flow intermittence across 8 alluvial rivers caused no increase in the observed loss of species richness, abundance, composition or functional trait composition and thus may have management implications. This suggests that in braided reaches of alluvial rivers, human-induced increases in flow intermittence (*e.g.* water abstraction) may have less of an influence on community richness than in rivers with more stable environmental conditions. However, it is likely that any anthropogenic activities, such as channelization, that decrease the mosaic of habitats within the floodplain of alluvial rivers will eliminate many of the sources of colonization that promote high community resilience. Additionally, land-use activities that increase the deposition of fine sediments which can clog the riverbed (*e.g.* agriculture, logging) will limit the capacity of the hyporheic zone to promote resilience. Managers must aim to preserve or restore three-dimensional connectivity to promote community resilience in alluvial rivers.

Management efforts aimed at minimizing the effects of climate change on aquatic communities should be prioritized to rivers where communities are less resilient to flow intermittence. It is more likely that communities comprised of taxa sensitive to disturbances becoming exacerbated by climate change are found in more environmentally stable rivers such as headwaters; whereas communities in braided reaches are likely to be more resilient to climate change because they are mainly comprised of resilient taxa. If management efforts are aimed at increasing community resilience to future climate change (Palmer *et al.* 2008), then minimizing disturbances is not likely to be successful (Côté and Darling 2010). Minimizing disturbances could increase community richness, but not likely resilience because the additional species may be more susceptible to disturbance.

7.2 The hyporheic zone as a primary source of colonization in alluvial rivers

In my manipulative field study in the Eygues River (Chapter 4), the hyporheic zone was the main source of colonization upon flow resumption, suggesting it can be a primary source of community resilience in alluvial rivers. While previous studies have either focused on the return of relatively few taxa from the hyporheic zone (*e.g.* Holomuzki and Biggs 2007, Kawanishi *et al.* 2013) or been performed at small spatial scales (*e.g.* Williams and Hynes 1976, Fowler 2002). My results provide the first empirical evidence showing that the hyporheic zone is a primary source of colonization for multiple taxa following disturbance at the community-level within entire river reaches. Despite preventing drift, which is often considered the most important source of colonization in rivers (Brittain and Eikeland 1988, Mackay 1992, Bilton *et al.* 2001, Altermatt 2013), community richness and composition across the 6 braided river reaches recovered within 1-2 weeks of flow resumption. This high resilience complements my findings across 8 braided alluvial rivers (Chapter 3 and Section 7.1)

and extends the current understanding of community resilience by identifying the primary process likely promoting high community resilience in alluvial rivers.

Identification of the hyporheic zone as a source of invertebrate colonization suggests it can act as a storage area of benthic invertebrates in alluvial rivers. Invertebrate 'storage' in the hyporheic zone can ultimately (i) protect species against local extinction (Mergeay *et al.* 2007), (ii) promote species diversity through coexistence (Chesson 2000) and (iii) influence the genetic structure of populations (Bohonak and Jenkins 2003). Species can become locally extinct in disturbance-prone systems like braided alluvial rivers if they have a limited dispersal ability (Levins 1969, Bohonak and Jenkins 2003, Reigada *et al.* 2015). For example, Bogan and Lytle (2011) found that a severe drought and subsequent river drying caused local extinction of three formerly abundant species that had low dispersal ability in desert streams that are isolated from any perennial rivers by a distance of 10 km. Most aquatic invertebrate species rarely move >5 km during their lifetime (Bilton *et al.* 2001) and long-distance dispersal is rare albeit difficult to quantify (Bohonak and Jenkins 2003). In my study, all abundant taxa (comprising 90% of total abundance) were found inhabiting the hyporheic zone during drying events eliminating the chance that dispersal limitation, in terms of distance to colonization source, could influence community resilience. This buffering effect of the hyporheic zone may become particularly important under future climate change scenarios which predict that the length of intermittent river sections will increase dramatically, further fragmenting dry river reaches from neighboring perennial habitats (Gleick 2003, Döll and Schmied 2012, Jaeger *et al.* 2014).

Invertebrate storage in the hyporheic zone could also enable the coexistence of competing aquatic species (*i.e.* the storage effect; Chesson and Warner 1981,Warner and Chesson 1985). Species coexistence via the storage effect occurs when (i) species traits buffer population growth rates during unfavorable conditions, (ii) there is covariance in competition and environmental conditions and (iii) responses to environmental variance are species-specific (Miller and Chesson 2009). First, population growth during favorable environmental conditions increases the persistence of populations during unfavorable conditions (*e.g.* disturbance). This is because there is a higher chance of survival by some individuals within the population and this subsequently 'fuels' population growth following the return of favorable conditions. In rivers, the likelihood of a species inhabiting the hyporheic zone increases with its abundance (*i.e.* mass effects; Leibold *et al.* 2004). As a result, species with high abundances have a greater chance of surviving drying and having higher population growth following flow resumption. Second, covariance between competition and environmental conditions typically occurs when species reach high abundance during favorable environmental conditions but subsequently face increased competition due to greater demands on available resources (*e.g.* food, space). In the hyporheic zone, however, the covariance relationship may be reversed because abundances are likely lower during favorable conditions (less competition) and higher during disturbances such as drying (more competition). Third, species-specific responses to environmental variance can create variability

in the abundance because species with low abundance can have an advantage over highly abundant species due to lower levels of competition (Miller and Chesson 2009). Indeed, species-specific responses to disturbance occur frequently in aquatic communities when some species have strategies of resistance and others of resilience (Leigh *et al* 2015). The hyporheic zone may further contribute to species-specific responses to disturbance by increasing survival in certain taxa that are able use the hyporheic zone as a refuge during disturbance. Therefore, the hyporheic zone is likely to influence the 3 conditions identified by Miller and Chesson (2009) needed to promote co-existence through the storage effect.

Finally, invertebrate storage in the hyporheic zone could influence the genetic structure of populations in rivers by reducing gene flow (*i.e.* the exchange of genes between populations; Bohonak and Jenkins 2003). Gene flow may be reduced if dispersal rates from outside populations are low or if immigrating individuals do not produce offspring. The former may be the case in isolated systems such as headwater reaches and arid-land streams (Phillipsen and Lytle 2012). By contrast, population connectivity in braided reache of alluvial rivers is considered high (Arscott *et al.* 2005) and therefore dispersal limitation is not a likely factor in these systems. In the latter case, however, the success of dispersing individuals can be low if early colonizers establish themselves and limit the genetic contribution of later colonizers (*i.e.* the monopolization effect; De Meester *et al.* 2002). De Meester *et al.* (2002) argued that a large seedbank (*i.e.* storage) of zooplankton species in ephemeral pools prevented newly invading genotypes because of founder effects and local adaptation to environmental conditions. I hypothesize that a similar effect could occur in alluvial rivers due to invertebrate 'storage' in the hyporheic zone during disturbance. In the Eygues River, recovery to pre-drying levels of invertebrate density occurred just 1 week after flow resumption and was driven by colonization from the hyporheic zone. The close resemblance of pre- and post-drying communities by the second week of flow resumption suggests that early colonizers could have outcompeted those that arrived later from other colonization processes. If these early colonizers did not have an advantage, I would have expected to see changes in community composition over time as taxa arrived from other sources, and this was not the case. Therefore, rapid colonization from the hyporheic zone following disturbance could potentially limit gene flow and influence genetic structure of populations in alluvial rivers.

The relative importance of the hyporheic zone as a source of colonization following flow resumption is likely to change depending on the location of the reach along the river corridor because of longitudinal differences in vertical connectivity (Figure 7.2). The ability to measure vertical migration of invertebrates from the hyporheic zone in my study was likely maximized by focusing the manipulative experiment in the braided reaches of an alluvial river, where vertical connectivity is highest relative to the headwater and meandering reaches (Ward and Stanford 1995). The persistence of invertebrate communities following drying in headwater and meandering reaches of alluvial rivers despite lower vertical connectivity implies that other sources of colonization (*i.e.* upstream or aerial

sources) are more important to community resilience in these reaches. In intermittent headwater reaches, it is unlikely that upstream sources of colonization would be available, unless perennial springs are present; therefore, I hypothesize that aerial colonization may be the primary source of invertebrate community resilience (Figure 7.2). As for meandering reaches that experience drying events, I hypothesize that drift from upstream will be the primary source of colonization promoting community resilience because these reaches have lower drainage density compared to small headwater reaches and therefore distances to neighboring aerial colonization sources may be prohibitive (Figure 7.2).

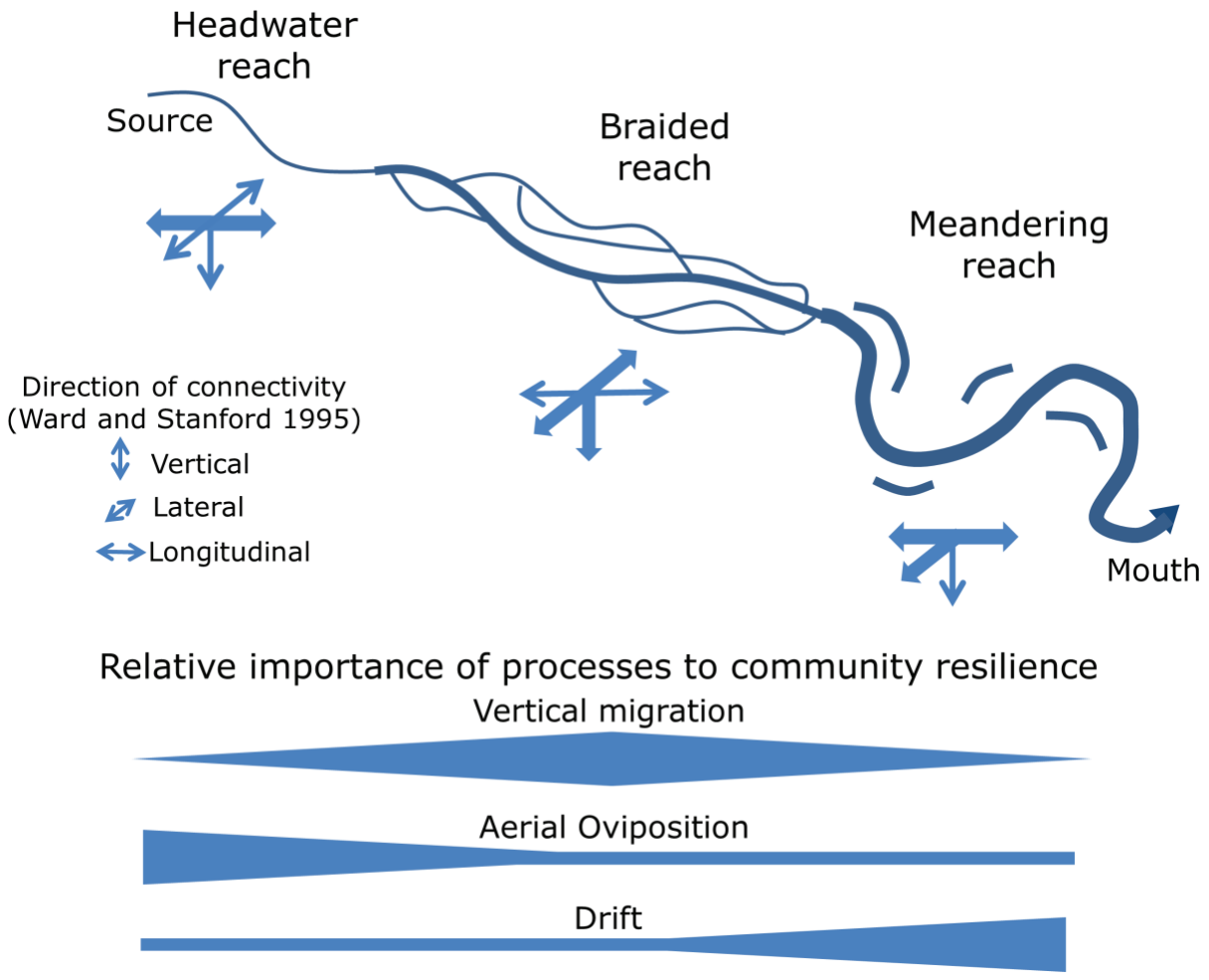

Figure 7.2 Predicted relative importance of vertical migration, aerial oviposition and drift as processes that promote community resilience in headwater, braided and meandering reaches of alluvial rivers. Direction (arrows) and strength of connectivity (arrow weight) are adapted from Ward and Stanford (1995).

7.2.1 Management implications

Identifying management actions that enhance the resilience of riverine systems is a major priority when seeking to minimize the impacts of climate change (Palmer *et al.* 2008). In braided reaches of

alluvial rivers, the hyporheic zone can be a primary source of colonization that promotes community resilience to river drying. Therefore management efforts in these reaches should focus on protecting or improving their surface-subsurface connectivity (Palmer *et al.* 2009, Boulton *et al.* 2010).

While protecting and restoring longitudinal connectivity has been an important management priority (Poff *et al.* 1997, Erős and Campbell Grant 2015), the vertical dimension of connectivity tends to be overlooked (Boulton *et al.* 2010). The hyporheic zone is threatened by many human activities, including agriculture, mining and flow regulation that lead to its clogging with fine sediments (Datry *et al.* 2014), limiting the vertical migration of organisms (Navel *et al.* 2010; Descloux *et al.* 2013; Vadher *et al.* 2015). Therefore management of alluvial rivers must consider these activities as potentially detrimental to the resilience of communities and the ecosystem functions they perform. The hypothesized shifting importance of sources of colonization along alluvial rivers suggests that flexible management approaches are needed to best focus management efforts to improve community resilience. Managers must consider what sources drive resilience in the system they are aiming to protect or restore. For example, protection and restoration efforts in braided alluvial reaches should focus on vertical connectivity, as mentioned above. However, in headwater reaches, actions should aim to protect or restore sources of aerial colonization, such as adjacent headwater streams, to maintain community resilience. In meandering reaches, protecting upstream sources of colonization and longitudinal connectivity that permit drifting and upstream dispersal of invertebrates should be prioritized.

7.3 Temperature and intraspecific competition initiate vertical migration into the hyporheic zone

I demonstrated in my first mesocosm experiment that *G. pulex* avoids increasing water temperatures and intraspecific competition by vertically migrating into the hyporheic zone (Chapter 5). However, migration into the hyporheic zone likely had negative consequences on their survival, feeding rates and energy stores. These findings inform our mechanistic understanding of the causes of hyporheic zone use by invertebrates during drying events by extending previous work on invertebrate migration into the hyporheic zone (*e.g.* Stumpp and Hose 2013, Vadher *et al.* 2015). Not only does migration occur upon the decline in water levels but my results show that invertebrates use environmental cues such as temperature and intraspecific competition to enter the hyporheic zone before surface water disappears. Knowledge of such cues is essential to identify thresholds that, if crossed, may drive changes in community persistence and ecosystem functions (Groffman *et al.* 2006).

Thresholds are important to identify before accurate prediction of the effects of climate change on biodiversity and ecosystem function can be made (Groffman *et al.* 2006, Bellard *et al.* 2012). Additionally, thresholds can serve as management objectives in river assessment, restoration and

protection schemes (Groffman *et al.* 2006, Dodds *et al.* 2010). Based on the results of my study, I predict that major changes in aquatic communities and ecosystem function will occur when surface water temperatures increase above 25°C. Not only was 25°C identified as the upper thermal threshold of *G. pulex* that caused migration into the hyporheic zone in my experiment, but many aquatic invertebrate species have upper thermal tolerances near 25°C and would likely migrate to find lower temperatures or face low reproductive success and mortality (Quinn *et al.* 1994, Stewart *et al.* 2013a). If invertebrates are unable to avoid the high temperatures, the ensuing population declines will alter community food webs (Thompson *et al.* 2013) and likely impact ecosystem functions, such as leaf litter decomposition (Datry *et al.* 2011).

In alluvial rivers in Mediterranean and temperate climate regions, surface temperatures frequently exceed 25°C during the warm summer months. For example, in the Eygues River, surface water temperatures ≥ 25°C occurred in many of my study reaches before complete drying. Vatland *et al.* (2015) reported that summer surface temperatures of around 25°C occurred in multiple reaches along an approximately 100 km section of an alluvial river (Big Hole) in Montana. However, alluvial rivers are thermally heterogeneous, driven largely by spatial and temporal variation in the surface-subsurface water exchange (Ward and Stanford 1995, Arscott *et al.* 2001). Reaches where water upwells from the hyporheic zone can be as much as 4.6°C cooler than in downwelling reaches (Capderrey *et al.* 2013). I posit that thermal heterogeneity along alluvial rivers likely creates hot spots of invertebrate migration into the hyporheic zone during summer months in areas where surface water temperatures rise above 25°C (Figure 7.3). These hot spots will likely be located in downwelling reaches and pools where surface water temperature peaks along the river corridor (Figure 7.3).

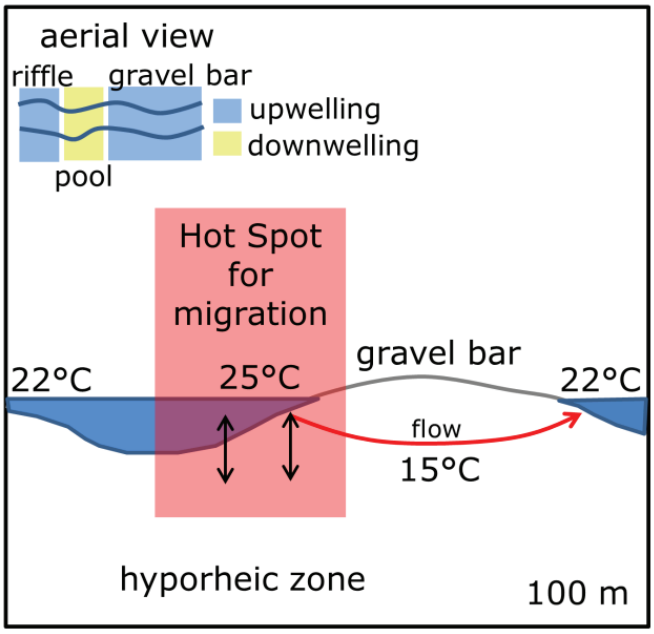

Figure 7.3 Potential hotspot of invertebrate migration into the hyporheic zone corresponding to a hypothetical gradient of water temperature during summer months in an alluvial river reach.

Surface water temperatures can also be extreme in rivers of other climate regions and climate change will exacerbate these extreme temperatures. In arid-land rivers, water temperature during summer months can average between 20–30°C with maximum temperatures reaching up to 40°C (Grimm and Fisher 1989, Boulton *et al.* 1992). Wallace *et al.* (2015) reported that water temperatures ≥ 28°C occurred during approximately 80% of the time period between October and January in two dryland waterholes in Australia. Climate change will exacerbate high summer water temperatures between 1–2°C, on average, by mid-century along with higher and more frequent maximum temperatures (Mantua *et al.* 2010, van Vliet *et al.* 2013). These increases in surface water temperature highlight the importance of habitats that mitigate the negative effects of temperature on aquatic organisms.

There is a strong need to identify and protect habitats that can mitigate the negative effects of climate change on biodiversity and ecosystem function (*i.e.* refugia, holdouts, stepping-stones; Ackerly *et al.* 2010, Keppel *et al.* 2012, Hannah *et al.* 2014). In aquatic ecosystems, the hyporheic zone can act as a thermal buffer that provides refuge from high surface water temperatures. Several previous studies have shown that invertebrates can survive prolonged periods of low flow and stream drying during droughts in the hyporheic zone (Wood and Armitage 2004, Stubbington *et al.* 2015). However, I have shown that there are trade-offs involved with hyporheic zone use (*e.g.* starvation) that can ultimately affect organism survival and decrease the capacity of the hyporheic zone to provide a thermal refuge. These trade-offs deserve more consideration by studies examining invertebrate use of the hyporheic zone.

7.3.1 Management implications

I found an upper temperature threshold that caused migration of *G. pulex* into the experimental hyporheic zone and this lead to a reduction in leaf litter decomposition. Thresholds (*i.e.* tipping points) have important management implications because they represent a point when an ecosystem changes dramatically in terms of community composition or ecosystem function (Groffman *et al.* 2006, Dodds *et al.* 2010). River managers can use thresholds as a reference to set management actions. For example, in the Big Hole River, Montana, recreational fishing activities are prohibited when water temperatures above 21°C are sustained for 8 h per day for 3 consecutive days to minimize stress on fish communities (Vatland *et al.* 2015). Management activities such as maintaining river flow and reforesting riparian areas, when applicable, can be used to keep water temperatures below 25°C and minimize negative effects on invertebrate communities (Rutherford *et al.* 2004). For example, high temperature spikes may occur more frequently during summer months in catchments with higher percentage of deforestation along the riparian corridor than in those where forested riparian buffers are left intact (Palmer *et al.* 2009). Thermal heterogeneity in alluvial rivers implies that fine-scale modeling of temperatures (Vatland *et al.* 2015) will be important to better determine where temperatures may exceed thresholds in these systems.

7.4 Water table depth reduces community resilience and alters ecosystem function

In my second mesocosm experiment, fewer organisms survived and returned to the surface when depth of the water table increased indicating this can be an important factor that limits hyporheic zone use by *G. pulex*. Consequently, leaf litter decomposition was reduced following the experimental drying events. My results emphasize the importance of integrating ecology and hydromorphology to explain the complex patterns and processes that occur in aquatic ecosystems (Vaughan *et al.* 2009, Poole 2010). In alluvial rivers, ecological and hydromorphological processes are linked through surface-subsurface exchanges of water that influence the vertical migration of invertebrates into the hyporheic zone, thereby affecting community composition and the breakdown of organic matter. Management and restoration efforts that incorporate knowledge of this link will promote community resilience and the maintenance of ecosystem functions (Lake *et al.* 2007, Palmer *et al.* 2008).

Water table depth varies greatly during drying events in alluvial rivers due to spatial variation in the elevation of the river channel and the groundwater aquifer (Larned *et al.* 2011, Datry 2012). In the Eygues River, water table depth remained 5−67 cm below the bed surface during the week-long drying events. However, water table depth can increase in channels perched above the alluvial aquifer (Capderrey *et al.* 2013). For example, water table depth ranged from 1−14 m below the riverbed in the Albarine River, France during drying events as a result of the river flowing from a confined gorge into

an unconfined alluvial plain (Datry *et al.* 2012). Alluvial rivers in the United States and New Zealand follow a similar pattern, becoming intermittent in unconfined river sections where the groundwater aquifer is > 4 m below the riverbed but remaining perennial where the river valley is confined (*e.g.* Larned *et al.* 2011). As the duration of drying events increases in alluvial rivers, the water table depth can decrease at rates between 1–9 cm day^{-1} (Clinton *et al.* 1996, Stella *et al.* 2010). Based on these rates, a 15-d increase in drying event duration, as predicted to occur by 2050 in the southwestern USA (Jaeger *et al.* 2014), could result in an additional 1.35 m (9 cm day^{-1}) increase in water table depth. This suggests that prolonged drying events associated with climate change have strong potential to negatively affect invertebrate community resilience by increasing the water table depth to levels inaccessible to benthic invertebrates.

7.4.1 Management implications

Increasing the water table depth during experimental drying decreases the survival and resilience of *G. pulex* as well as its contribution to leaf litter decomposition. These results indicate that prolonged drying events, such as those predicted due to climate change and water abstraction, could have negative effects on the capacity of the hyporheic zone to promote community resilience. The quantitative relationship I determined between survival and increasing water table depth of *G. pulex* populations indicates that beyond a water table depth of 1 m there would be 100% mortality of these populations. More work must be performed to develop and test similar relationships for other common benthic invertebrates that use the hyporheic zone to persist in intermittent rivers. This knowledge could be used by managers to predict where the potential contribution of the hyporheic zone to community resilience is threatened (assuming water table depth measurements are available during drying events) and thus inform management prioritization.

7.5 Perspectives

7.5.1 Community resilience across gradients of environmental harshness

The conventional view in disturbance ecology is that taxonomically and functionally diverse communities are more resilient to natural disturbances than those depauperate communities, such as those in environmentally harsh systems (Silver *et al.* 1996, Yachi and Loreau 1999, Côté and Darling 2010). However, an alternative view predicts communities in harsh systems will be more resilient because these communities should be dominated by taxa with strategies for resistance and resilience (Silver *et al.* 1996, Côté and Darling 2010, Baskett *et al.* 2014) and that these strategies enable taxa to co-tolerate several types of disturbances (Vinebrooke *et al.* 2004). Under this alternative view, communities should become less taxonomically and functionally diverse but the proportion of resistant

and resilient taxa relative to sensitive taxa should increase along gradients of increasing environmental harshness. Empirical evidence from coral reefs (Coté and Darling 2010), marine fisheries (Neubauer *et al.* 2013) and tropical forests (Cole *et al.* 2014) has provided support for these relationships but generalizable evidence in lotic systems is lacking. This is despite the broad range of environmental harshness gradients that have been previously studied in lotic systems (*e.g.* flood, Lepori and Malmqvist 2007; drying, Datry *et al.* 2014; glacial influence, Jacobsen and Dangles 2012, Cauvy-Fraunie *et al.* 2014). A meta-analysis using datasets gathered from previous studies across different environmental harshness gradients could reveal broad-scale patterns in taxonomic and functional diversity across lotic systems, while exploring the diversity-stability relationship.

7.5.2 Testing the importance of interspecific competition under benign and harsh environmental conditions

One of the primary mechanisms that explain species coexistence via the storage effect (*i.e.* temporal recruitment fluctuations that enable stable coexistence; Chesson 2000) is covariance in the strength of competition and environmental conditions (Miller and Chesson 2009). Theory suggests that under benign and stable environmental conditions competition for food resources and/or space should be at its highest; whereas, competition should decrease under harsh environmental conditions (Grime 1973, Chesson and Huntly 1997, Violle *et al.* 2010). However, empirical evidence of this relationship in aquatic communities has provided mixed support (*e.g.* Hemphill and Cooper 1983, Jiang and Morin 2004) and few studies have considered how use of the hyporheic zone by invertebrates could either reduce or strengthen competition and contribute to species coexistence through the storage effect. For instance, interspecific competition for food resources, such as leaf litter, on the surface can increase as environmental conditions (*e.g.* temperature) become more harsh because organisms increase their feeding rates to compensate for higher metabolic needs (*e.g.* Jiang and Morin 2004). Under such harsh conditions, however, competition can be reduced if organisms are able to migrate into the underlying hyporheic zone where more favorable and stable conditions could lower their metabolic needs. On the contrary, competition could increase if two competing taxa enter the hyporheic zone where food and space are inherently more limited than on the surface. Testing how interspecific competition is influenced by environmental harshness and exploring the role that the hyporheic zone plays in this process are important steps in understanding species coexistence in alluvial rivers.

An experiment could test the relationship between environmental harshness using two competing species (*e.g. G. pulex*, *Leuctra*) in mesocosms with or without access to the underlying hyporheic zone. Benign and harsh environmental conditions on the surface could be created by manipulating water temperature (*e.g.* 15°C, 25°C). The strength of competition could then be measured using feeding rates of the two competing species, quantified using nitrogen stable isotopes (*e.g.* Navel *et al.*

2011), growth rates of organisms and glycogen content. Each species should be tested separately and together across both levels of environmental harshness to ensure that observed changes in feeding, growth rate and glycogen content are due to competition. Species (*G. pulex*, *Leuctra*, *G. pulex* + *Leuctra*) × harshness (control, high) × hyporheic zone (yes, no) treatment combinations could be replicated (n = 3) across 36 mesocosms. I hypothesize that in the absence of an accessible hyporheic zone, invertebrates would have a reduction in feeding rates, growth rates and glycogen content, indicating increased competition. By contrast, in treatments where invertebrates have access to the hyporheic zone, a lack of difference between mono-species and competition treatments in feeding rates, growth rates and glycogen would indicate reduced competition resulting from more benign conditions in the hyporheic zone.

7.5.3 Assessing population-level variability in the response of invertebrates to drying

Population-level variability in the response of species to disturbances can result from local adaptation (Kawecki and Ebert 2004, Violle *et al.* 2012) and hinder our ability to make accurate predictions of future changes to communities (Feckler *et al.* 2014). In my second laboratory experiment, I aimed to address population-level variability in the response of populations of *G. pulex* from one intermittent and one perennial river to drying. There were no differences in the resilience of these two populations to drying; however, there was a strong preference for hyporheic zone by the population originating from the perennial river. Combined with other studies that have shown population-level variability (*e.g.* Chapuis and Ferdy 2012, Foucreau *et al.* 2014), it remains necessary to consider variability between populations in intermittent and perennial rivers in more depth in future experiments.

Future studies could explore population-level variability in aquatic invertebrates across Mediterranean and continental climate zones using a common garden approach (*i.e.* simultaneously subjecting different populations to the same stressor; Kawecki and Ebert 2004). Multiple populations from perennial (n = 10) and intermittent rivers (n = 10) should be selected for experimentation. Populations could then be subjected to various treatment factors including desiccation resistance, thermal tolerance and refuge seeking ability in the hyporheic zone. I hypothesize that if drying is a selective force that affects population structure, then strong differences in the response to these treatment factors should occur between populations originating from perennial and intermittent rivers. This may elucidate the subtle differences found in previous studies.

7.5.4 Developing a tool to manage the hyporheic zone in alluvial rivers

A major goal in the management of aquatic ecosystems is to protect and/or restore the resilience of communities and ecosystem functions (Lake *et al.* 2007, Palmer *et al.* 2008). In this thesis, I showed

that the hyporheic zone is a primary source of community resilience in alluvial rivers and growing evidence suggests it serves an important role in biogeochemical processes, such as respiration, nitrification, methanogenesis and associated ecosystems services (Boulton *et al.* 2010, Krause *et al.* 2011, Griebler and Avramov 2015). Therefore, consideration of the hyporheic zone is critical to achieve management goals in aquatic ecosystems. Yet, to effectively manage the hyporheic zone, clear direction as to where the hyporheic zone contributes to these processes is required (Malard *et al.* 2002, Tonina and Buffington 2009, Mermillod-Blondin *et al.* 2014).

A combined mapping (GIS) and modeling approach based on recent geomorphological developments (Buffington *et al.* 2004, Snelder *et al.* 2011, Helton *et al.* 2014) can be applied to construct a tool that allows managers to identify river reaches with high or low potential of the hyporheic zone to contribute to biological processes including community resilience. Aerial photographs and digital elevation models can be used to identify confined and unconfined alluvial river valleys, resembling beads on a string (sensu Stanford and Ward 1993), which indicate the strength and direction of surface-groundwater exchanges (Malard *et al.* 2002, Capderrey *et al.* 2013). To estimate hyporheic zone potential, substrate size can be modeled (*e.g.* Snelder *et al.* 2011) to identify reaches with coarse substrates that allow vertical migration of invertebrates. Hydrological characteristics such as river flow and water table depth should also be considered to estimate river drying duration and maximum depth to the water table that limit survival of invertebrates in the hyporheic zone (Snelder *et al.* 2013). Finally, land-use information could provide estimates of potential threats to surface-groundwater connectivity, such as sedimentation that occurs from agricultural and logging activities to help target management plans. Creating a GIS platform such as EstimKart (Snelder *et al.* 2011) that combines these geomorphology, hydrology and land-use data (Figure 7.4) will allow river managers to prioritize their efforts to protect and restore surface-groundwater connectivity to promote resilience to future climate changes and anthropogenic pressures.

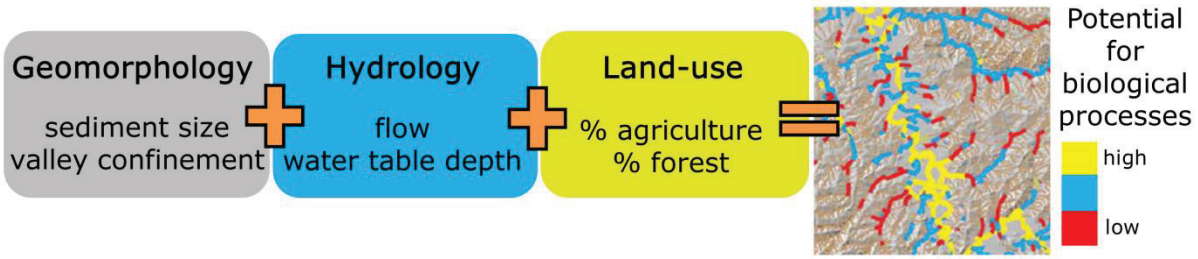

Figure 7.4 Proposed mapping and modeling approach to construct a GIS tool that allows managers to identify river reaches with high or low potential to contribute to biological processes including community resilience.

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